

AMERICAN MUSEUM *Novitates*

PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2547 SEPTEMBER 24, 1974

LESTER L. SHORT

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LESTER L. SHORT

*Curator, Department of Ornithology
The American Museum of Natural History
Adjunct Professor, City University of New York*

AMERICAN MUSEUM NOVITATES

NUMBER 2547, pp. 1-42, figs. 1-5, tables 1, 2
Issued September 24, 1974
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ISSN 0003-0082
Price. \$2.62

ABSTRACT

Field studies of the little-known Black-backed Three-toed Woodpecker (*Picoides arcticus*) and the Northern Three-toed Woodpecker (*P. tridactylus*) during part of a breeding season in northern New York yielded much new information about the habits of the former species and some comparative data regarding the latter. Both species occur in the vicinity of spruce bogs where *arcticus* is more conspicuous and generally dominant over *tridactylus*. *Picoides arcticus* forages in dead trees, especially low dense or fallen trees, and *tridactylus* in live evergreen trees, generally higher up. The foraging sounds of *arcticus* were louder than those of *tridactylus*. Nest excavation, brooding, nest sanitation, and the feeding and behavior of nestlings are discussed for *P. arcticus*. Nestlings called almost continuously throughout the day. The female fed the young more often than did the male, but the male carried more food items per trip, and performed most of the nest sanitation. There are two distinct forms of drumming in *P. tridactylus*, both slower in tempo than the drumming of *arcticus*; drumming of these species is compared with four other sympatric woodpeckers. A Kyik Call (call note), Screech Call, five calls of a Yeh Call complex, Kyik-ek Call, Snarl Call, Rattle Call, and distinctive Scream-Rattle-Snarl Call are described for *arcticus*. Calls of *tridactylus* discussed are the Pik (call note), the Rattle, and the Kweek. Vocalizations of these picids are compared, and the comparison is extended to closely related (and sympatric) *P. villosus* and *P. pubescens*. Three bill positioning postures, a Hunched Posture, Crest Raising Display, Head Bobbing Display, Head Swinging Display, Wing Spreading Display, Flutter Aerial Display, and Tail Spreading Display are described for one or both three-toed woodpeckers. Conspecific interactions, encounters between *tridactylus* and *arcticus* and conflicts of *arcticus* with *villosus* and other species are discussed. The data support the relationship of *arcticus* and *tridactylus* with the North American assemblage of *Picoides*. They further suggest that *tridactylus* has diverged less, and *arcticus* more from their common ancestor. Specialization of *arcticus* as it evolved in a milieu of related North American congeners probably was a factor permitting *tridactylus* to invade North America successfully from Eurasia in the recent past.

INTRODUCTION

The Black-backed and Northern Three-toed woodpeckers (*Picoides arcticus* and *P. tridactylus*, respectively) are among the least known of North American woodpeckers (see Taylor, 1958, and Kilham, 1966, for *arcticus*; *tridactylus* is best known from Europe, see especially Ruge, 1968, 1971; Gibbon, 1966, provided some North American data). Although both species range across the continent, they frequent dense, boreal forests, which has discouraged study. Their distribution suggests extensive sympatry and their ranges do overlap extensively, but these closely related picids rarely have been found together. Rather, in the regions within the area of sympatry, one species is common to uncommon and the other is uncommon to rare. Thus, when I became aware that Mr. Ferdinand La France had found both species nesting beside a bog in the Adirondack Mountains of New York during 1971 and 1972, I adjusted my schedule to permit field studies in the area during 1973.

The present report documents the results of field investigations during a 16-day period in late April to early May and in mid-June of 1973, around Eagle Creek Bog, 4 miles northeast of Eagle Bay, elevation 1780 feet, in Hamilton County, New York. A considerable volume of data was gathered despite the brief time of my studies. The data are based on observations, with use of 10 by 50 field glasses, and analyses of tape recordings of three-toed woodpecker vocalizations obtained during the field work. The recordings were made with a Uher 4000-L Report Tape Recorder and a Phillips directional microphone and analyzed from sonagrams produced by a Kay Electric Company Sound Spectrograph. Additional comparative data, including tape recordings and sonagrams of *Picoides pubescens* and *P. villosus*, were obtained by Mr. Jay Barry, Mr. Kent Fiala, and Ms. Sally Baier, National Science Foundation Undergraduate Research Program students at the Kalbfleisch Research Station of the American Museum of Natural History, Dix Hills, Huntington, Long Island, New York. Background information and comparative data were available from results of my earlier

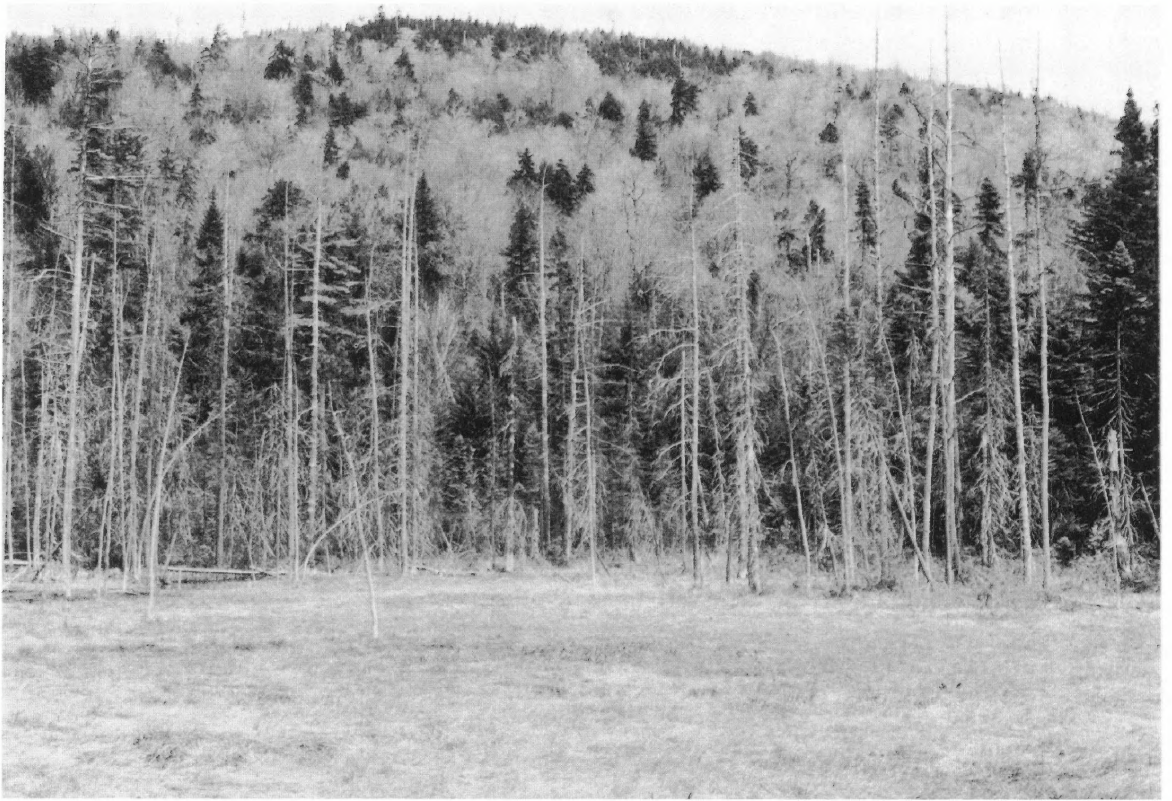


FIG. 1. Open portion of Eagle Creek Bog, Hamilton County, New York, where both species of three-toed woodpeckers occurred. To the northeast, is a line of dead trees in which *Picoides arcticus*, especially, and *P. tridactylus* forage. Here, bordering spruce-larch forest is restricted by slope and its mixed coniferous-hardwood forest. Slopes support populations of *Dryocopus pileatus*, *Picoides villosus*, *Sphyrapicus varius*, and to a lesser extent, *Colaptes auratus*. Photograph taken April 29, 1973.

studies of related North American (Short, 1971), European (Short, MS), and Asian species of *Picoides* (Short, 1973). The taxonomy used herein follows that of Short (1971).

I thank Mr. La France for information concerning the three-toed woodpeckers at the study site, and for a tour of the area in late April, 1973. I also acknowledge the help of Mr. John Bull, who provided valuable information, and Mrs. Sheila Short and Miss Penny Short, who assisted during part of the field work.

Description of the Study Site

Eagle Creek Bog is a spruce-bordered marsh and pond in rolling hills forested with mixed

hardwoods and conifers (beech-maple-hemlock forest) on slopes, and dense spruce and larch woods in areas of poor drainage. The pond covers 10 acres bordered by open bog (featuring many pitcher plants) and some standing dead stubs, the open area extending over about 30 acres (fig. 1). The spruce-larch forest surrounds the open bog, but in several places where these adjoin there are stands of open to dense stubs. Other such "dead tree" stands, none extensive, border Eagle Creek westwardly. The dead trees probably resulted from flooding due to recent damming activities by beavers.

In late April, 1973, Mr. La France pointed out to me the 1972 nest sites of a pair each of *P. arcticus* and *P. tridactylus*. The former nest was

in a stub within a rather dense cluster of dead trees southwest of the pond and its surrounding open bog. The nest of *P. tridactylus* was in a stub standing in mixed live and dead trees at the edge of forest east of the bog, about 400 meters from the *arcticus* nest. At least *P. arcticus* had nested in the bog in 1971 as well as in 1972.

During late April and early May, 1973, an estimated five Black-backed and three Northern Three-toed woodpeckers were active in the bog and the surrounding spruce-larch forest. Despite almost daily heavy rains and snow on two (of 11) days, woodpecker and other avian activity was great, and territorial and other intraspecific and interspecific encounters were frequent. Six picids occurred commonly about the bog—the two three-toed woodpeckers, Yellow-bellied Sapsuck-

ers (*Sphyrapicus varius*), Pileated Woodpeckers (*Dryocopus pileatus*), Common Flickers (*Colaptes auratus*), and Hairy Woodpeckers (*Picoides villosus*). When I returned to the bog on June 11, I found that Northern Three-toed Woodpeckers, despite their earlier activity, no longer were in evidence. However, two pairs of *P. arcticus* were present, and one nest (fig. 2), begun in late April, was active. Other bog and forest birds also were nesting, and commonly seen were all three species of "*Melospiza*" (*melodia*, *georgiana*, *lincolnii*).

Morphology and Field Identification

The North American three-toed woodpeckers are closely related to each other and show great



FIG. 2. Site of Black-backed Three-toed Woodpecker nest in Eagle Creek Bog, Hamilton County, New York. Male woodpecker is visible partway up the large dead stub (arrow) in the center of the photograph. Dense spruce forest borders dead trees in background, and Eagle Creek is in foreground. Photograph taken April 29, 1973.

similarity. (Although not directly related to *Picoides*, Asian woodpeckers of the genera *Sasia*, *Gecinulus*, and *Dinopium* also are "three-toed.") The North American three-toed woodpeckers in external morphology differ in size, structure, and color, and *P. arcticus* has a more massive and much larger bill. The Black-backed Three-toe generally is about one-quarter larger than the Northern, averaging about 70 grams in weight compared with 56 grams for the Northern (weights from about 80 museum specimens representing mainly western North American populations of the two species, supplied chiefly by Ned K. Johnson). Their difference in size is apparent in the field only when both species are observed together.

The three-toed woodpeckers resemble each other most closely in coloration in eastern North America, because *P. tridactylus bacatus* tends toward *P. arcticus* in having reduced barring on the back. Indeed, some museum specimens of *P. t. bacatus* show but a few white spots or spot-bars on the back, which would appear "black" in the field. I find also that barring of the outer tail feathers, ordinarily very restricted in *P. arcticus* and extensive in *P. tridactylus* so varies that there is considerable overlap, accentuated (the least barred outer rectrices are obscured) under field conditions.

Characters useful in field identification of these woodpeckers are: The Black-backed Three-toed Woodpecker is blacker, that is, more "glossy" and less brown than the Northern. Its facial markings are sharply contrasting, with a clear white connection from the subocular stripe across the lores to the area just above the nostrils. The subocular white stripe is broader posteriorly and tends to isolate the black malar stripe. It lacks white spots on the tips of the secondary and tertial feathers, an excellent field mark. When seen in good light, the Northern Three-toed is browner dorsally and less contrastingly black and white than is *P. arcticus*. The subocular white stripe of *tridactylus* is narrower, thus the black malar stripe broadly meets the black side of the neck. The loreal area and forehead just over the bill are mixed white and black, gradually grading into the forehead and anterior malar stripe. The secondaries and tertials are tipped with white, showing lines of white spots down

the wings when the bird has its back to the observer. Of course, any birds so barred-backed as to appear "ladder-backed" in the field can be identified as *P. tridactylus*. Males of *P. arcticus* show a more anteriorly placed yellow crown patch, which is more "neatly" bordered with black than in *P. tridactylus*.

Behavioral traits discussed below also may aid in field identification, especially the call notes and rattle-like calls, which are diagnostic.

Habitat and Ecology

I found the Black-backed Three-toed Woodpecker frequenting more open areas about the Eagle Creek Bog than did the Northern Three-toed. Black-backs used dead trees for foraging and drumming, and they moved from stub to stub in areas with dead trees. The Northern Three-toed seemed to employ dead stubs as drumming sites, but not for foraging. Both species tend to allow humans to approach rather closely, but the Black-back often challenges the intruder, whereas the Northern darts away into the forest. These habits plus the fact that Black-backs are more vocal than Northern make *P. arcticus* much more conspicuous. These differences may be local rather than general for the two species, and possibly they are influenced by interspecific competition between them.

Foraging differences between *P. arcticus* and *P. tridactylus* in the Adirondack Mountains during the spring are illustrated by comparative observations made on May 4. I encountered a male and female *P. tridactylus* foraging together high on the trunk of a spruce, the female about a half meter above the male. Both individuals tapped and especially probe-tapped laterally, flaking off pieces of bark. As the male moved upward, the female remained in place, excavating for two and one-half minutes. Both paused frequently, remaining quiet. Fifty meters away a female Black-back foraged low in a broken, dead spruce, tapping loudly and directly, not laterally. Time and again it excavated in flurries, sporadically extracting large white larvae. Tapping and excavating of *P. arcticus* are louder than foraging noises made by *P. tridactylus*, although this may be due partly to the usually dry, hard dead wood in which *arcticus* taps, compared with the damp,

live wood in which *tridactylus* more commonly excavates.

Black-backed Three-toed Woodpeckers often forage very low in either dead or live trees, and occasionally (11 incidents) hop about the ground, tapping at dead branchlets and at the bases of dead trees (see Kilham, 1966, p. 309). On May 1 a male *arcticus* excavated and tapped, boring deep into standing dead or dying small spruces near the edge of the bog. Its mate hopped about the ground 8 meters away, probing into the bases of trees and crevices, and tapping at fallen branches using both straight and lateral blows. Later the same day I saw a female 8 meters up a large, live birch tree, excavating and dropping big pieces of bark for about 4 to 5 minutes. On June 11 a female hopped about the edge of Eagle Creek, darting about and probing into loose pieces of wood and crevices, almost frantically seeking food for its young in a nest nearby. Even in large, live trees, *P. arcticus* usually forages very low, and indeed the female I noted above feeding in a birch tree was the highest at which I observed this species to forage.

I observed that Northern Three-toed Woodpeckers foraged higher in trees and more often in live trees than did Black-backs. I failed to observe *tridactylus* in dense, low dead spruces and larches, or feeding along fallen branches and trunks where *arcticus* commonly was encountered. *Picoides tridactylus* taps and excavates less loudly than does *arcticus*. Stallcup (1962) noted that the food of *tridactylus* consists largely of Coleoptera, especially of the family Scolytidae, but also Cerambycidae, Buprestidae, and Pythidae. I saw no indication of sapsucking, or of the ringing of trees reported for *tridactylus* in Europe by Turček (1954, p. 34) and Ruge (1968, pp. 117, 118).

Both species foraged entirely in the bog and adjacent to it in spruce-larch forest, avoiding surrounding drier slopes containing mixed hardwoods and conifers, where *P. villosus* was common. I found no consistent sexual differences in foraging in either three-toed species.

NESTING OF *PICOIDES ARCTICUS*

Nest Excavation

The future nest was discovered at 06:50 on

April 26, when I encountered a female Black-back tapping within a hole 4 meters up a dead spruce 12 cm. in diameter, situated almost on the bank of Eagle Creek amid a group of 10 or 12 dead stubs (fig. 2). The cavity entrance faced northeast, toward the creek and was beveled on the lower portion, so that the hole slanted slightly upward. Freshly bared areas above and below the entrance suggested that large pieces of loose bark had recently been removed from the tree, presumably by the woodpeckers. At 07:00 the male arrived at the site, replaced the female, and began excavating within the hole, which was deep enough only to admit his head and bill.

Over the next several days both birds, but mainly the male, excavated intermittently. By early morning of April 28, the birds could put almost half their body into the cavity. On April 30, when I risked checking the nest somewhat frequently I found the female excavating at 07:00, well into the opening, but still bracing her tail. Thereafter, the male was excavating at 08:30, 10:00, 12:00, 13:00, and 15:10. The female "visited," interacting with the male, and looking into the cavity at 13:00 and 15:10, but did not excavate. By 11:00 on May 1, the male no longer propped its tail, but worked well into the cavity, with only the tail and wingtips protruding. On May 2 the male worked at 16:00, with only the tip of the tail outside the hole, and obviously excavating downward from the entrance tunnel. The male excavated on May 3, between 06:20 and 09:20, with breaks of 32 and 13 minutes, and continued beyond 09:20. At 11:00 on that day the female visited the nest, entered, and, for the first time, turned around inside to peer out of the entrance. She then worked inside the cavity for seven minutes. On May 4 the male excavated prior to 09:15, and continued beyond 11:15. The nest was completed after that day and contained young birds on June 10.

Before they could turn about in the cavity, the woodpeckers backed out of the entrance to toss away chips of wood. Later they put their heads outside the cavity, and shook away the chips.

Thus, both sexes participate in nest excavation, although most of the labor is done by the male.

Nest Approach

Most often the adults flew directly to the nest entrance from all directions. Generally they landed just below the entrance, but occasionally they came to one or the other side of it, and, infrequently, above the nest. Whenever either adult flew to a point a meter or more above the cavity, it did not back down, but dropped off the stub in flight, and flew to the entrance.

Brooding of Nestlings

The young birds were moderately well developed by June 10, and little brooding occurred during the day. Also, it generally was warm during the time of my visit. The female remained in the nest for several (up to 4) minutes after feeding on a few occasions. On June 11, the male brought food at 08:11, and remained 17 minutes in the nest, probably brooding, until the female appeared with food. Again on June 15, a cool day, the male brooded for 10 minutes early in the morning, leaving when the female arrived, displaying to the male. The male spent the night of June 11 in the nest, and probably the night of the twelfth. On June 14, however, the male fed the young for the last time at 20:13, then flew far to the east, near the pond, where I had seen a freshly excavated hole in a stub. I remained until dark, after the calls of the young birds had quieted down (after 20:47). I returned at 05:00 the next morning (June 15), and no bird left the nest. Rather, the first feeding occurred at 05:28 (by the female), and the male appeared with food at 05:30. Thus, by June 14 the male no longer remained all night in the nest with the young as he had previously.

Nest Sanitation

As with most woodpeckers, fecal sacs are removed from the nest by the adults. In the Black-backed Three-toed Woodpecker these sacs are removed at intervals, carried to a perch, usually in the vicinity of the nest, then flung to one side. I did not see a sac dropped while either adult was en route from the nest, but only after the bird reached a perch. The male removed the great majority of the sacs, even returning to the nest in quick succession to remove two, three, or (once)

five consecutive droppings, thus suggesting that five young birds occupied the nest on that day, June 14. The male entered the nest on 88 out of 166 visits during the 1933 minutes I observed the nest between June 11 and 15. On at least 83 of the 88 occasions he removed one (or more) fecal sacs from the nest, thus doing so on 50 percent of his visits. The female entered the nest only 18 times to feed, and often remained in the nest (possibly to brood) for a short time, but she removed a fecal sac only seven times. Thus, the female removed fecal sacs on only 3 percent of her 234 visits. The male removed 12 times more sacs than did the female, thus bearing out Kilham's earlier (1966) observations of nest sanitation by the male only.

Feeding of Young

I was able to observe feeding of perhaps five nestling Black-backed Three-toed Woodpeckers on June 11 to 15, 1973. Based on such factors as the frequency of feeding of the young, cessation of feeding inside the nesting cavity, cessation of roosting nightly in the nesting cavity by the adult male, and frequency of brooding (Ruge, 1971, presented data for *P. tridactylus*), I estimate the age of the nestlings at between 10 and 18 days during the period of study. Observations covered 1933 minutes, varying from 236 minutes on the morning of the eleventh, to 630 minutes on June 14. During the period of observation, the male and female fed the nestlings 400 times.

Feeding was accomplished almost entirely at the nest entrance. During the early part of the period (June 11, 12), the adults occasionally placed the head and part of the body inside the entrance tunnel. On rare occasions they entered the nest briefly to feed the young. In the latter part of the study period adults entered the nest only to remove fecal material, and they invariably left the nest carrying a fecal sac. Longer periods in the nest, presumably for brooding, were rare, the longest being for 17 minutes on June 11.

The method of feeding varied little, the adult turning the head laterally to place the bill partly within, and perpendicular to, the bill of a nestling. This mode has been described for *arcticus* (Taylor, 1958, fig.; Kilham, 1966) and *tridactylus* (see fig. 8 in Ruge, 1971). Food items

brought to the nest include diverse insects; adults and larvae were seen frequently in the bills of the adult woodpeckers. Kilham's (1966, p. 308) observation that females, which generally feed the young more frequently than do males, carry fewer items of food is corroborated by my studies. The female I observed carried fewer insects, fed fewer nestlings per visit, and completed feeding more rapidly than did the male. The bill of the male much more frequently was obviously crammed with insects. Often the feeding male paused, then appeared to cough up more food which was then fed, frequently to a nestling other than that fed previously. It is possible that insects are carried in the esophagus, as well as in the mouth, for the male's "coughing" action resembles that of woodpeckers like *Colaptes auratus* that regularly regurgitate food to their young. Of course the male sometimes carries few food items to the nest, and even forages occasionally adjacent to the nest, securing and carrying a single insect to the nestlings. The female only rarely appears to have the bill filled

with food, and I saw her "cough" up more items on only two occasions. It would be worthwhile to investigate whether this difference in feeding the young is a reflection of sexual differences in foraging or in the kinds of insects that are taken.

Most feeding observations occurred mornings, but I accumulated sufficient data to present a reasonably clear view of hour-by-hour feeding throughout the day (table 1). There is an initial surge of feeding early in the morning, which continues at a moderately high level through much of the morning. Midday marks a definite slowdown, for a period of about three hours. There follows an increase to a moderate level in the late afternoon. There is no increase in feeding before nightfall; rather there is a slight drop from the late afternoon rate. Although I observed great hourly fluctuations in the feeding rate, longer periods of about two hours showed remarkable day-to-day similarity throughout the five days, despite differences in weather conditions. For example, there were 35 feedings the first two hours of June 12, a warm day, and in the same

TABLE 1
SUMMARY OF FEEDING AT NEST OF *PICOIDES ARCTICUS*
DURING FIVE CONSECUTIVE DAYS^a

| Time ^b | Minutes of observation | Feedings | Average time between feedings ^c | Average feedings per hour |
|-------------------|---------------------------|----------|--|------------------------------|
| 06:00 | 210 | 69 | 3.02 | 19.71 |
| 07:00 | 240 | 47 | 5.07 | 11.75 |
| 08:00 | 180 | 33 | 5.27 | 11.00 |
| 09:00 | 170 | 43 | 3.59 | 15.18 |
| 10:00 | 230 | 46 | 5.00 | 12.01 |
| 11:00 | 120 | 23 | 5.13 | 11.50 |
| 12:00 | 59 | 11 | 5.22 | 11.22 |
| 13:00 | 90 | 12 | 7.30 | 8.00 |
| 14:00 | 115 | 19 | 6.03 | 9.82 |
| 15:00 | 55 | 8 | 6.52 | 8.55 |
| 16:00 | 90 | 18 | 5.00 | 12.00 |
| 17:00 | 135 | 28 | 4.49 | 12.44 |
| 18:00 | 75 | 14 | 5.21 | 12.00 |
| 19:00 | 60 | 9 | 6.40 | 9.00 |
| 20:00 | 43 | 8 | 5.22 | 11.11 |

^aJune 11 to 15, 1973, Eagle Creek Bog, Hamilton County, New York.

^bTime shown is Eastern Daylight Saving (EDT). Each hour listed covers the hour from 30 minutes before to 30 minutes after, e.g., 06:00 = 05:30 to 06:30.

^cIn minutes.

period on June 15, a cool day, there were 34 feedings. Two midmorning hours on warm June 11 had 23 feedings, and there were 22 feedings the same two hours June 15. The maximum number of feedings in one hour was 24 between 05:25 and 06:25 on June 15, and the minimum was four between 15:11 and 16:11 on June 13.

Various data indicate clearly the greater frequency of feeding by the female Black-back. Of 400 feedings, 234 (59%) were by the female and 166 by the male, with daily percentages for the female varying between 54 and 63 percent. In 29 separate hours during which the nest was observed for the full 60 minutes, the female fed the young more frequently than did the male in 22 of the hours, both fed the same number of times in five of the hours, and only in two of the hours did the male feedings exceed those of the female. Further, in 1933 minutes of observation the male stayed away from the nest 20 times for periods of more than 15 minutes (15-67 minutes, average 31.55 minutes), whereas the female spent 18 to 65 minutes (average 30.3 minutes) away from the nest on only seven occasions. During the times when the male was absent the female fed the young every 6.37 minutes, carrying the full feeding load at a rate of 9.41 feedings per hour. In contrast, during the seven prolonged absences of the female, the male fed the young every 8.55 minutes at a rate of 7.1 feedings per hour. The male averaged an extended break from feeding every 1.61 hours, and the female, every 4.6 hours. Finally, I found that of 386 cases for which the sex of the adult is known in consecutive feedings the sexes alternated 213 times (55.2%), the female fed consecutively 118 times (30.6%), and the male followed itself in feeding only 55 times (14.2%). Despite the greater frequency of feeding by the female, the fact that the male carries, on the average, more food items (perhaps three to four times as many) than the female, suggests that the male easily provides half, perhaps even two-thirds, of the food for the young.

These data suggest that unless the female changed her mode of feeding, she could not by herself feed the number of young found in this nest, whereas, if she disappeared during the nestling period, the male could successfully feed the young in this nest. An estimated eight feedings

an hour by the male would sustain the young, and of course he broods the young at night until late in the nestling phase; the female, using her present feeding modes, would have to sustain a rate of 15 or 16 feedings an hour, and she does not roost and brood the young in the nest at night. To be sure, lesser feeding rates would suffice to rear fewer young than the four or five in the study nest.

England's (1940) report of a nesting *arcticus* in California provided some feeding data from one day, although only the midday hours were treated in detail. From 08:00 to 11:00 he noted visits alternately by the sexes with intervals of less than five minutes between visits, i.e., at a rate of more than 12 feedings per hour. There were six feedings (three by each sex) in 55 minutes between 11:00 and noon, and five feedings (three by the female) in 29 minutes around 13:00. These data are roughly comparable with those reported herein.

Kilham (1966) studied two nestings of *arcticus* in New Hampshire. In both cases the adult female fed the young more frequently ("about three times" as many visits as males, Kilham, 1966, p. 308) than did the male. Although Kilham remarked on the variation in number of visits, he gave no data on the total number of feedings he observed, but they may be about one-tenth the number I have reported, as Kilham observed only seven instances of nest sanitation. Nevertheless, Kilham's and my observations suggest a general difference between the sexes in feeding of nestling Black-backed Three-toed Woodpeckers.

The available data from *Picoides tridactylus* indicate that females of *tridactylus* play a weaker role in feeding the young than do females of *arcticus*. Gibbon (1966) discussed a New Brunswick nest of *tridactylus* which, at about the same stage of nesting as the *arcticus* nest above, involved 2.36 times more feeding by the male than by the female. The number of feedings (72) reported in the eight-hour period from 04:30 to 12:30 is 73 percent of the average figure for the *arcticus* nest I studied. Lanz (1950), reporting on European *tridactylus*, showed many substantial feeding gaps of up to two or more hours. Feeding rates he noted, covering parts of four days over an eight-day period, were at a rate of

from less than two to four feedings per hour, with periods of more than seven hours in which only the male fed the young. The great preponderance of feedings was by the male. Ruge's data (1971) from observations of five European *tridactylus* nests indicate that both sexes feed about as frequently early in the nestling period, but the rate of the female generally diminished until, late in the period, she ceased feeding altogether (in four or five nestings). These reports suggest that there may be a difference between *arcticus* and *tridactylus* in the role of the female in feeding the young.

Kilham (1966, p. 310) noted that *Picoides villosus* resembles *P. arcticus* in that the females feed the young more frequently and carry less food per visit than do males.

Behavior of Nestlings

The aggressiveness of young *Picoides arcticus* was noted by both Kilham (1966, p. 309) and me. The constant vocalizations of the nestlings (see below) seem to be one reflection of their aggressiveness. Another is the difficulty encountered by adults entering the nest for the purpose of sanitation. The nestlings, waving and hitting with the bill, so besieged the adult that it often had to make several attempts before successfully "running the gauntlet" into the nest. Perhaps this aggressiveness is a factor in determining when the adult male ceases his roosting in the nesting cavity. When they feed the young, adults often seem forced to turn aside momentarily in order to avoid the thrusting bills of the nestlings. Bourdo and Hesterberg (1951) also called attention to the aggressive nature of young Black-backs. The method of feeding, in which the adult turns its head perpendicular to that of the young to be fed (see above), seems to lessen the risk of injury. I find no mention of such aggressiveness in young Northern Three-toed Woodpeckers.

DRUMMING

Both three-toed woodpeckers employ the familiar woodpecker instrumental signal termed drumming to a degree greater than in most other woodpeckers, and drumming is especially prevalent in *Picoides tridactylus*, which shows struc-

turally and seemingly functionally distinct types of drumming. Data are available from analysis of sonagrams of 81 drumming bouts of *P. arcticus*, and 35 of *P. tridactylus*. Comparative data are available for related *P. scalaris*, *P. nuttallii*, *P. pubescens*, and *P. villosus*, including five cases of drumming of the last species in and around the New York bog where I studied the three-toed woodpeckers, and for three other unrelated, sympatric woodpeckers in the vicinity of the bog. I note, however, that the data represent only a small part of the year, and that there may be seasonal variation in such aspects as the frequency of drumming by the two sexes, the frequency of different types of drumming, and in the duration and average number of beats per instance of drumming.

Picoides tridactylus

Drumming episodes of this woodpecker (table 2) involved seven to 27 beats (average 15.77) lasting 0.67 to 1.83 seconds (average 1.24 seconds). The drumming can be categorized as fast, moderate, or slow in tempo. The moderate and fast drumming bouts form a continuum, with three subcategories: fast with a terminal speedup (20 cases), moderate with a terminal speedup (five instances), and moderate without a change in tempo (two cases). The first of these subcategories encompasses the majority of drumming that I heard. These averaged 14.3 beats per second (fig. 3B, F), delivered in 1.30 seconds, containing 18.55 beats. The second subcategory averaged 12.71 beats per second, in 1.01 seconds, and 12.80 beats. These two subcategories show a 25 percent increase in tempo, from an average of 13.13 beats per second in the initial one-half second of the bouts to 16.39 beats per second in their terminal one-half second. The final subcategory, moderate without a change in tempo, averaged 12.2 beats per second in 1.2 seconds, and averaged 14.5 beats per bout. These "typical" drums are used in response to drumming either by conspecific birds, or interspecifically, as to drumming *P. arcticus*. Presumably they serve as a territorial proclamation (aggressive), and perhaps a localization function. Data from central European *P. tridactylus* (Ruge, 1968, pp. 120-121) indicate drumming essentially like that of

TABLE 2
DATA SUMMARIZED FOR DRUMMING OF SIX SPECIES OF *PICOIDES*

| Species | Location | N | \bar{X} Beats | \bar{X} Duration in seconds | \bar{X} Beats per sec. | Tempo Change ^a |
|--------------------|-----------------------|----------------------|--------------------|--|-----------------------------------|------------------------------|
| <i>tridactylus</i> | New York | 8 | — ^b | — ^b | 8.95 | 0 |
| <i>tridactylus</i> | New York ^b | 27 (35) ^b | 16 | 1.24 | 13.84 | +25% |
| <i>pubescens</i> | New Jersey, New York | 27 | 14 | 0.93 | 16.36 | 0 to -5% |
| <i>arcticus</i> | New York | 81 | 27 | 1.45 | 18.83 | +17% |
| <i>nuttallii</i> | California, Mexico | 58 | 21 | 1.06 | 19.08 | 0 |
| <i>villosus</i> | New Jersey, New York | 10 | 23 | 0.90 | 25.96 | 0 to -5% |
| <i>scalaris</i> | California | 5 | — | < 0.50 | 30.00 | 0 |

^a Average percentage change in tempo from first half-second to last half-second.

^b Slow drum bouts (first line) differ from moderate and fast bouts (second line) only in tempo, hence are included in second line of *tridactylus* (total N=35) under the fourth and fifth columns. See text.

Symbols: N, number of bouts; \bar{X} , mean.

these "typical" New York drummings in all respects.

Slow drumming (fig. 3C) involved eight episodes, seven of which averaged 8.76 beats per second (showing no overlap with fast to moderate drums), delivered in 1.31 seconds, and containing 11.43 beats per bout. These steady, slow drums showed no change in tempo. One slightly faster burst, at 10.3 beats per second, lasted 0.78 second and contained eight beats which slowed perceptibly through the call. Slow drumming probably was used mainly intraspecifically, for it occurred between members of a pair. These bouts elicited no response from other picid species nearby. Thus, there are two main types of drumming in this woodpecker, and they seem to differ functionally, although more data are needed to prove this.

Picoides arcticus

In the course of the field work several hundred drums of Black-backed Three-toed Woodpeckers were heard. The quality of the drumming varied from site to site. The male of one pair regularly used a drumming site in a stub 3 meters from the nest, and 5 meters above ground. This favorite site, marked by a cluster of 15 to 20 small holes, was used for about one-third of the drumming activity of this male. Otherwise, all

birds observed showed no preferred site. Although certain prominent stubs were used most frequently, drumming was not restricted to specific sites in the stubs. Many instances of drumming occurred almost casually in dead or live trees where birds happened to be when motivated to drum. Indeed, away from the nest tree and its associated stubs the woodpeckers usually exhibited no tendency to seek an optimum drumming substrate.

Drumming bouts were irregular and rarely prolonged following the onset of nesting. Mornings were by far the prime time for drumming, although the amount varied greatly from morning to morning. Once nesting commenced, the series of bouts diminished. After that, usually four or five bursts were the maximum rendered by a bird before flying off.

During five days in June in which I spent 1933 minutes observing the nesting pair of Black-backs, I noted 84 series of drumming bouts. Of these, 55 were single, 14 double, 11 contained three bursts, and in four instances there were four separate bouts, giving 132 drumming bouts. Much of this drumming presumably was elicited by my continuous proximity to the nest (prior to completion of the nesting cavity in early May, there was less drumming in response to my presence). Other bursts were elicited by the arrival of the mate when one adult was already at the

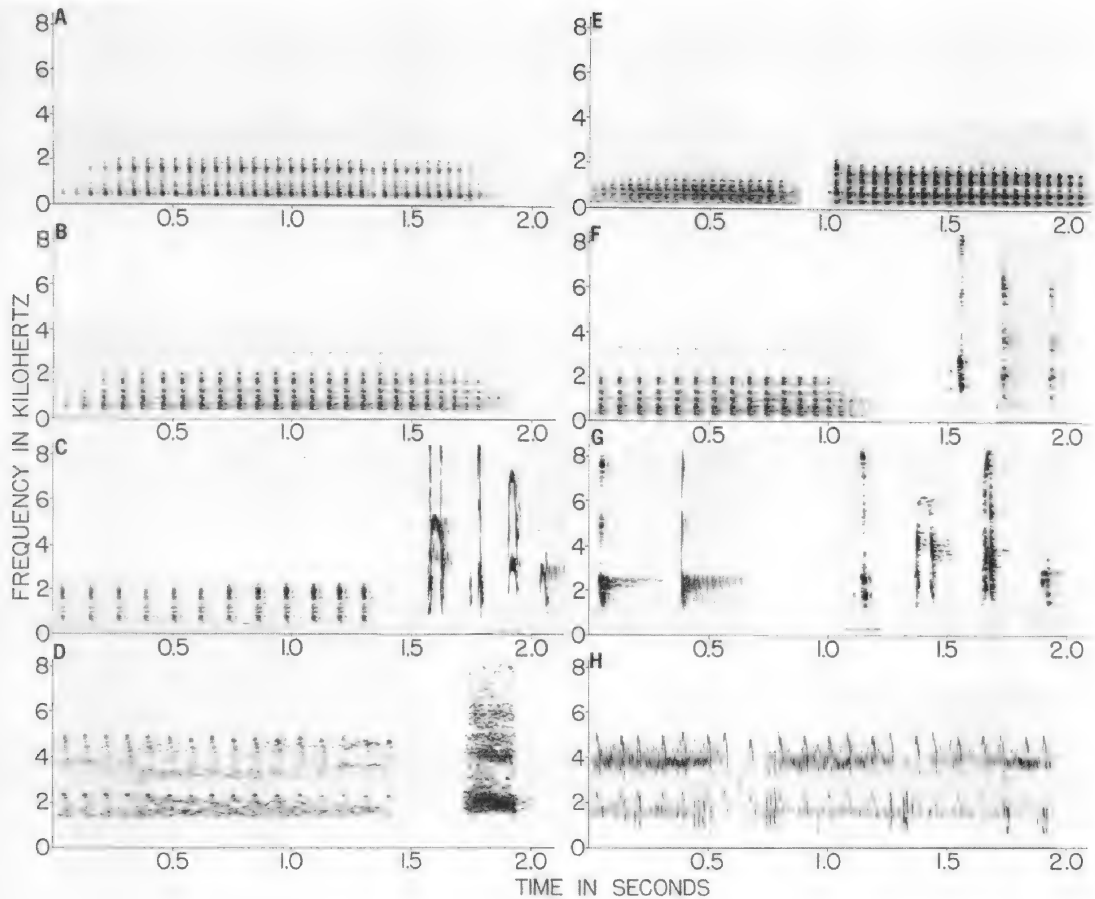


FIG. 3. Sound spectrograph of drumming and calls of *Picoides arcticus*, *P. tridactylus*, *P. villosus*, and *P. pubescens*. A. Drumming of male *arcticus*. B. Fast drumming of male *tridactylus*. C. Slow drumming of female *tridactylus*, 12 beats, followed by single call notes, WB, respectively of *villosus* (Peek Call), *arcticus* (Kyik Call, notice preliminary element), *pubescens* (Pit Call), and *tridactylus* (Pik Call). D. Long Screech Call of adult *arcticus*, with background (tall, distinct notes) nestling Slow Rattle Call (notice diffuse sound tending to consolidate toward end of Screech Call at 3.8 and 4.2 kilohertz), followed by one of a series of type III distress calls of female *pubescens*, for comparison with Screech Call. E. Drumming of male *villosus* near nest 1/3 mile upslope from the *arcticus* nest, then drumming of female *arcticus*. F. Fast drumming of male *tridactylus*, then single Kyik Call of *arcticus* (notice skewedness of note at right, and faint lead element) to be compared with following two notes, notes 7 and 8 of a 20-note precopulatory Tewk Call of *villosus*, uttered near nest. G. Kyik Call of female *arcticus*, variant note with intense, terminal tail of sound, followed by same note, WB, then single call notes respectively of *arcticus* (Kyik Call), *villosus* (Peek Call), *pubescens* (Pit Call), and *tridactylus* (Pik Call). H. Screech Call of *arcticus*, series of three bursts with background (tall notes) nestling Slow Rattle Call and (also tall notes) Yeh-kk Calls; notice Screech Call tendency to form discrete band toward end of bursts at 3.8 kilohertz, WB. All sonagrams narrow band unless indicated wide band by WB, from recordings obtained in New York State, mainly in Hamilton County, except calls of *pubescens* and (one) *villosus* from Long Island.

nest. Excluded from consideration at this time are drumming bursts occurring during the same five-day period of June, but either away from the nest, or near the nest as part of a display sequence involving conspecific individuals other than the mate, or birds of other species.

The 84 cases of drumming near the nest in June took place during 76 of 319 morning visits, and eight of 81 afternoon visits, thus 76 percent of the total of 400 visits to the nest, but 90 percent of the drumming occurred in the morning. Furthermore all the drumming series involving more than two bouts, and most of those having two bouts occurred in the morning. There was considerable daily variation in drumming, with a minimum of 9 percent of the visits to a maximum of 40 percent involving drumming bouts on various days. The male drummed more than the female on four of five days, performing 52 (62%) of the 84 drums, and all but four of the multiple drum series. Because the male was the less frequent visitor, he actually drummed more than twice as often (on 52 of 166 visits, 31.3%, compared with 32 drums in 234 visits, or 13.7%, by the female). These data contrast with Kilham's observations of two pairs in New Hampshire, where the females drummed more often, and more frequently drummed several times in succession than did males.

I analyzed 81 drumming bouts of *P. arcticus* with the use of sonagrams (fig. 3A, E). About half of this number represents drumming by a mated male and female feeding young at the nest during the five days of study in June. The remainder was recorded in late April and early May, or in June, but not at the nest site, and represents as many as four or possibly five individuals. The 81 bouts include 41 drums by males, 28 drums by females, five drums ascribed to males, five to females, and two bouts not ascribable to either sex.

In contrast to *P. tridactylus* there were no discrete categories of drumming. I segregated three groups of male drumming bouts and four groups of female bouts based on their pitch (high, medium, and low in males; high, medium, low, and diverse in females), but found no consistent differences within each sex. This was anticipated, for the pitch of drumming is affected by the nature of the substrate used for drumming, and

the birds seemed to utilize diverse sites opportunistically. There was a strong tendency for a difference in drumming between the sexes, with females employing about as many or more beats in less time on the average, thus showing a faster tempo. Four samples of male bouts gave average tempos of 17.61, 18.11, 18.11, and 18.19 beats (overall average 18.01 beats), compared with 19.80, 19.82, 20.09, 19.60, and 20.52 beats (overall average 19.95 beats) for five samples of females. However, males show such variability in duration of the bouts, in the number of beats contained, and in tempo, that they overlap completely with females. Further data nevertheless probably will demonstrate that a difference exists between the sexes in the tempo and duration of drumming. The samples for both sexes when pooled (table 2), show on the average 27.11 beats (range 11 to 36), lasting 1.45 seconds (range 0.58 to 2.03 seconds), with an average tempo of 18.83 beats per second (range 16.22 to 22.45 beats per second) for the 81 bouts analyzed.

A speedup in tempo through the drumming bursts is characteristic of this species as well as of *P. tridactylus*. All drums of *P. arcticus* that were analyzed show such a speedup. Omitting the eight of 81 drums that were less than one second in duration, there was a speedup in tempo of from 1.0 to 5.5 beats per second between the initial one-half second and the terminal one-half second of the other 73 bouts. The average increase in tempo was 2.93 beats per second.

Interspecific Comparisons

The drumming of *Picoides tridactylus* and *P. arcticus* is compared with other congeneric species in table 2 (see also fig. 3). The distinctly different slow and fast drums of *tridactylus* are treated separately; the lesser, average, sexual difference in *arcticus* is ignored in that table. It must be stressed that as the samples are relatively small and seasonally limited, only general comparisons are attempted. The data suggest that tempo differences in drumming between species, and changes in tempo during drumming may be two parameters of importance in species discrimination, or otherwise are of such importance as to be species-specific (see also Short, 1971). Espe-

cially interesting are differences between the sympatric or potentially sympatric eastern species. *Picoides villosus* (fig. 3E) and *P. pubescens* (Short, 1971, fig. 23A), broadly sympatric, tend to show a slowdown in rate of delivery during a burst of drumming. However, based on the limited samples available, they differ in tempo, *villosus* being more rapid in its delivery. Sympatric *P. arcticus* and *P. tridactylus* differ significantly in the tempo of the beats, *tridactylus* giving slower bursts, generally somewhat shorter in duration, and containing fewer beats. Both *arcticus* and *tridactylus* show a strong speedup in tempo through a drumming bout. The differences between *arcticus* and *tridactylus* are about of the magnitude of those apparently occurring between *pubescens* and *villosus*.

In the New York study area *villosus* occurred adjacent to the bog frequented by *tridactylus* and *arcticus*. Interactions among these species were noted, and it is clear that they sometimes react interspecifically to drumming. Drumming differences may tend to reduce these interactions. Data suggest that *villosus* differs from *arcticus* in its drumming to about the same degree, but in the opposite direction that *tridactylus* does from *arcticus* (*villosus* drums 37% faster than *arcticus*, which drums 36% faster than *tridactylus*). It is noteworthy that *pubescens* was not encountered at the study site and that its drumming resembles that of *arcticus* and *tridactylus* more than does that of *villosus*. *Picoides pubescens* is smaller than *tridactylus* and the very aggressive *arcticus*, and its drumming may be sufficiently like theirs to cause interactions detrimental to itself. The large size and more different drumming of *villosus* may favor its partial coexistence with *arcticus* and *tridactylus*. Further data concerning the sympatric occurrence of *pubescens* and *villosus* with either or both of *arcticus* and *tridactylus* are needed to test the view that *villosus* ought to be found much more frequently than *pubescens* coexisting with the three-toed species.

As three other woodpeckers were sympatric with *Picoides tridactylus*, *P. arcticus*, and *P. villosus* in the study site, it is of interest that their drums are distinctive. *Sphyrapicus varius* drums in slow but usually very long bursts, often containing double beats. Its drumming is diagnostic,

easily distinguished from that of the other species. *Colaptes auratus* drums rather weakly, but in even, steady cadence, without change in tempo, at a rate of 22.16 beats per second, over 0.5 to 1.4 seconds. There is a resemblance to the drumming of *Picoides villosus*, but the drums are weaker, and show no slowdown; lack of a speed-up renders drums of *C. auratus* distinct from the usually slower drumming *Picoides arcticus*. Drums of *Dryocopus pileatus* usually are much louder and more resonant than those of the other five sympatric picids, and are delivered at a rate of 15.3 beats per second over 0.6 to 2.1 seconds. They are characterized by a speedup of 18 percent. *Dryocopus pileatus* thus resembles in its drumming the three-toed woodpeckers (Kilham, 1966, p. 308, remarked on this), falling between *Picoides arcticus* and *P. tridactylus* in rate of delivery, and resembling *arcticus* in the change in tempo. In the field, however, loudness usually renders the drums distinctive.

VOCAL SIGNALS

Several vocalizations of *Picoides tridactylus* and many of *P. arcticus* were tape-recorded. These, together with unrecorded calls heard and described in my field notes form the basis for an analysis of vocal signals in these species. The details presented are important for further intraspecific and interspecific studies and comparisons. It is hoped that they will stimulate other investigators to pursue functional analysis of these vocalizations. The various sounds are grouped tentatively into structurally based categories that apparently have functional bases as well. Within each category the discussion centers about *Picoides arcticus*. *P. tridactylus* is mentioned in relation to *arcticus* whenever the data warrant it.

Calls of Nestling Birds

The calls of nestling three-toed woodpeckers are somewhat variable, and a general summary of such calls will have to suffice pending full analysis and comparisons. The main call of most young woodpeckers is a rapid, rattle-like series of notes rendered variably as single notes, definite groups of notes, or long bursts or "rattles."

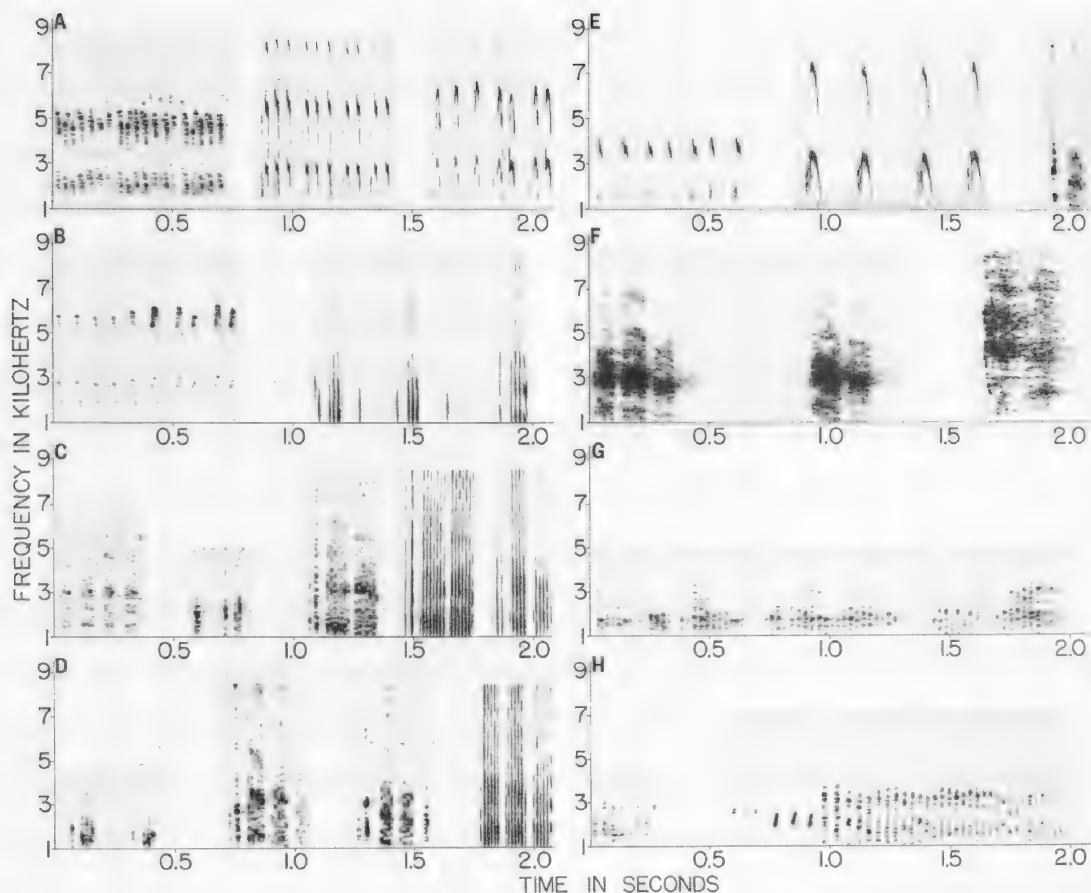
There generally is a close similarity between the individual notes and call notes of adults, and between series calls and rattle calls of adults. This is the case in *Picoides arcticus*.

The Rattle or Begging Rattle Call of young Black-backed and Northern three-toed woodpeckers has elicited remarks by many authors (e.g., England, 1940; Taylor, 1958; Erskine, 1959; Kilham, 1966, for *arcticus*; and Lanz, 1950; and Gibbon, 1966, for *tridactylus*), for unlike most picids the young of these two species call continuously or almost continuously. Indeed, this is how their nests are often located. It appears that the continuous calls represent one or sometimes two young birds. When the adult approaches the nest, usually all the young call more loudly, using different notes. It is not

known if nests containing fewer young are less noisy—hunger may be a factor prompting continuous calling by the hungriest nestling.

The buzzing, repetitive calls of young *Picoides arcticus* can be categorized into Fast Rattle (fig. 4A), Moderate Rattle, and Slow Rattle Calls (figs. 3D, 4A, B). The last can be subdivided into single-noted, and multiple-noted calls. During the five days devoted to studying the *arcticus* nest, there was a definite shift from Fast to Slow Rattle calls. The notes of all these calls are very much alike.

First Rattle Calls (fig. 4A) were uttered in series of four to seven notes given at intervals of about 0.05 second. Each note is about 0.02 second in duration, with sound diffuse at various frequencies, but usually showing a faint peak at



2.5 to 3.2 kilohertz. The notes are uttered at an average rate (10 bursts) of 28 notes per second (26 to 32 notes per second). There is variation in emphasis and frequency from note to note within a call. When adults appeared to feed the young, the Fast Rattle Call became louder and almost continuous, that is, with weak notes separating the strong bursts. Also there is more emphasis on higher frequencies in the food-begging Fast Rattle in the presence of an adult.

Intermediate between Fast and Slow Rattle calls are Moderate Rattles. These are like the Fast Rattle Calls in that notes are in bursts or series, but the tempo is less, at 16 to 22 notes per second. Other interesting features of this call are the tendency for a slowdown within each burst as it progresses and the initial note of a burst to differ from other notes in having a separate vertical element preceding it. The fundamental tone of these calls shows a peak at 2.5 or 2.6 kilohertz.

The Slow Rattle Call in its single-noted form (fig. 4A, B) consists of long bursts—for minutes at a time—of fast, vertical notes, given at regular intervals. Notes are variable in duration, from

0.015 to 0.04 second. The sound is diffuse generally, but with multiple points of emphasis giving a banded appearance under narrow-band spectrographic analysis. The fundamental tone usually shows a peak at 2.3 to 3.2 kilohertz, with a strong, and usually dominant, harmonic tone peaking at 4.6 to 6.3 kilohertz. The form of the notes is of a tight, inverted V, but with diffuse sound connecting at intervals the “legs” of the inverted V. Many notes are asymmetrical, with the peak skewed toward the beginning of a note, and with emphasis on the downward-dropping leg. As in the initial note of the Moderate Rattle, the Slow Rattle notes are generally preceded by a faint vertical element; this lead element is emphasized in the fundamental tone even when the harmonic tone is otherwise dominant. Notes of 10 randomly selected bursts show a delivery rate of 13.65 notes per second (range 12 to 15 notes per second). This persistent “di-di-di-di” call was that heard when no adults were at the nest in the later part of the five-day study period (i.e., June 13 to 15).

During feeding of the young late in the study

FIG. 4. Sound spectrograph of some calls of *Picoides arcticus*, *P. villosus*, and *P. pubescens*. A. Nestling Fast Rattle Call of *arcticus* (note tendency to group in bursts), then a series of two triple notes and two double notes from a nestling Slow Rattle Call of *arcticus*, WB, and finally a portion of a nestling Slow Rattle Call of *arcticus* showing a shift from single (first three) to double (last two) notes as the adult female commences feeding the nestlings, WB. B. Nestling Slow Rattle Call of *arcticus*, shift from single notes (1-4) to louder notes 5 and 6, to double notes (last two, each a pair of elements) as adult arrives and commences feeding, followed, WB, by Yeh Complex notes, to wit, a Yeh-kk Call (four elements), then a yeh note, another Yeh-kk Call (four elements), a yeh note, and finally a Yeh-kk Call (five elements), forming a sequence given by a male or female *arcticus* during an encounter. C. Series of four Yeh-yeh Calls of *arcticus*, then yik note (note resemblance to Kyik Call) and Yeh-kk Call (three elements) of Yeh Complex of *arcticus*, followed by three Kyik-ek Calls (three-note version, kyik-ek-ek) of *arcticus*, the first with long ek notes (notice “double” introductory kyik note), the second as the first but WB, and the third, WB, a Kyik-ek Call with shorter ek notes. D. Two Yeh-kk Calls (yeh-kek, four-note version), followed by three Kyik-ek Calls (note fine “banding” in ek notes), the first a four-note (kyik-ek-ek-ek) version, the second a peculiar three-note version with appended yik note (kyik-ek-ek-yik), and last, WB, a three-note form lacking initial kyik note (ek-ek-ek; notice banded terminal element). E. Seven notes of long nestling begging Rattle, *villosus*, WB, followed by four notes of nestling Slow Rattle of *pubescens*, WB, then two-note Kyik-ek Call of female *arcticus*. F. First two (of eight) odd Kyik-ek Calls, lacking kyik element, of 10-second series uttered by adult *arcticus* leaving encounter with *tridactylus*; compare with following, variant type III distress call of adult *pubescens*. G. Series of Snarl Calls of *arcticus*, interacting pair. H. Rattle-Snarl Call of male *arcticus*, followed by full Scream-Rattle-Snarl Call of female *arcticus* (notes 1 to 5 are scream notes, 6 to 10 are rattle notes, 11 to 38 are snarl notes). All sonagrams are narrow band unless indicated wide band by WB. Sonagrams from recordings obtained in New York State, mainly in Hamilton County, but also (*pubescens* and *villosus*) on Long Island.

The Pik Call of *tridactylus* sounds like "pik," "kik," or "peep," very much resembling the Pit Call of *P. pubescens* (see also Short, 1971), but distinctly less metallic than the Kyik Call of *arcticus* and less sharp than the loud Peek Call of *P. villosus* (fig. 3C, G). Characteristic of the Pik Call is its dominant fundamental tone and very weak or absent harmonic tones. The note appears on a sonagram as an inverted, U-shaped note, peaking at 2.8 to 3.0 kilohertz. Most sound is on the upper legs and peak of the fundamental tone, between 1.5 and 3.0 kilohertz. Notes are 0.03 to 0.035 second in duration. There tends to be a slight tailing of sound beyond the peak and a vague vertical band of sound immediately after the peak rising to perhaps 4 kilohertz. Harmonic tones are absent in four of five examples, with traces of one at 6.0 kilohertz. This call is shorter than the 0.035 to 0.05-second Pit Call of *pubescens*, and it is pitched lower than the 3.3 to 3.9 kilohertz (fundamental tone) peak of that Pit Call. Lacking the strong, even dominant harmonic tone of the Pit Call, the Pik Call of *tridactylus* thus has its sounds much lower pitched. Nevertheless, the general form of the two calls is similar.

The Kyik Call of *P. arcticus* (fig. 3C, F, G) is a rapid, metallic-sounding note, its form on a sonagram being a vertical column with many points or bands of emphasis between 1.5 and 8.5 kilohertz. Spectrographic analysis discloses that the note is in the form of a very tight, inverted V, with main emphasis on the dropping leg of the V. This accounts for the slight skewness of the vertical column toward the latter part of the note. When detectable, the peak of the fundamental tone is at 2.5 to 3.0 kilohertz. Harmonic tones about 5.2, and especially, 7.7 kilohertz often are prominent, though not dominant. The note usually is 0.02 to 0.023 second in duration; a few, more skewed notes are up to 0.03 second in duration. A moderate "tail" of sound often (fig. 3C, G) extends 0.2 to 0.3 second beyond the note at 2 to 4 kilohertz. Some notes (fig. 3C, F) are preceded by a faint vertical column. This column possibly could represent the vestigial rising leg of an originally broad note, the dropping leg of which has become the main note of the current Kyik Call. Such a broader note would closely resemble the Peek Call (fig. 3C, G) of *P.*

villosus without a definite peak. It is noteworthy that the apparently very different call notes of *villosus* and *arcticus* have peaks (when they are strong enough to be seen) at the same frequencies, that is, a fundamental tone peak at 2.5 to 3.0 kilohertz and corresponding harmonic tones at 5.0 to 6.0 kilohertz and above 7.5 kilohertz.

The constricted, metallic Kyik Call of *arcticus* differs markedly from the longer, softer Pik Call of *tridactylus*, as well as from the comparable calls of *villosus* and *pubescens*. The difference among these congeneric species in their call note is not surprising in view of the importance of this call (see above) and the sympatry among them (see also information on call notes of *P. scalaris* and *P. nuttallii* in Short, 1971, and of several Asian congeners in Short, 1973). As mentioned above, there is a possibility that the Kyik Call is a constricted version of an ancestral call note much like that of *P. villosus*. This possibility, or its evolution from other than an ancestral call note, is suggested too by its similarity to the lead note of some variant Tewk Calls of *P. villosus* (see fig. 3F). The Pik Call of *tridactylus* is longer, usually higher pitched, and definitely peaked with major emphasis on the fundamental tone. Field experience indicates that there is no difficulty whatsoever in distinguishing *arcticus* and *tridactylus* by their call notes. The Pit Call of *pubescens* (fig. 3C, G) is still longer and higher pitched, as well as peaked in comparison with the call note of *arcticus*, and the initial harmonic tone often is dominant. *Picoides villosus* has a call note (fig. 3C, G) longer yet than that of *pubescens*, with a muted fundamental tone and a dominant peak of the initial harmonic tone, and it has a strong terminal tail of sound.

Screech Call

Several bursts of low "screeching" were heard from adults at the nest of *Picoides arcticus*. This call is peculiar, and the only resemblance I have found with known calls of its relatives is one of the three types of distress calls of *Picoides pubescens*. This latter, screechlike call (fig. 3D) is a diffuse form of long, spectrographically horizontal note, given singly or in series by adult Downy Woodpeckers when they were held for banding on Long Island, New York.

The Screech Call of *arcticus* (fig. 3D, H) is a semi-continuous vocalization, usually a series of very diffuse notes barely connected by weaker notes, but sometimes continuous (fig. 3D). In calls that showed distinct series (fig. 3H), the notes varied within the range of 0.48 to 0.60 second in duration, with shorter intervening intervals (each about 0.15 second). A note generally is diffuse within the range of 1.5 to 5.0 kilohertz, but there is emphasis about 1.4 to 2.2 kilohertz (presumed fundamental tone) and 3.1 to 4.8 kilohertz (initial harmonic tone). In some cases the harmonic tone is dominant, and in other examples the fundamental tone is dominant. There is a tendency for an increase in loudness through each note, coupled with the forming of more discrete, horizontal bands at the fundamental and harmonic "peaks" toward the end of some notes.

The Screech Call is lower pitched, with less diffuse higher pitched sound, and the notes are less discrete than in the distress "screech" of *pubescens* (fig. 3D). The distress screech of *pubescens* is shorter, 0.2 to 0.35 second in duration, with definite gaps between notes. Emphasis is at about 2.5 and 4.5 to 5.0 and 7.0 kilohertz, but the sound is diffuse between those frequencies more than in the Screech Call of *arcticus*.

Yeh Call Complex

A variable array of usually very soft notes, vertical in form spectrographically, make up the Yeh Call Complex of *Picoides arcticus*. The various notes are rendered in my journal as "yeh" or "ya," "yik," "yeh-yeh" or "yek-ek," "yeh-kkk," and "kkkk." I tentatively treat these as equivalents of the Tewk Call of other *Picoides* (see Short, 1971, pp. 88-89). The various Yeh Calls are uttered during encounters between members of a pair near a nest (hence many recordings bear confusing background calls of the nestlings), and probably between individuals in many intraspecific encounters. Several different subcalls of this complex may be given alternately or irregularly in series, or various of them are rendered along with Snarl Calls or other calls during encounters. At this time I cannot assign functions to the variant calls of this complex, except to state that they appear to indicate aggression and perhaps

submission of individuals during encounters at very close range; sexual functions also may be served.

Yik Notes (fig. 4C): These are Kyik-like notes, infrequently uttered in combination with Yeh-yeh and Yeh-kk calls, or with Yeh notes. They are fast (0.02 second), weak, vertical notes with sound at intervals between 0.8 and 3.0 kilohertz. Six of eight examples sufficiently clear to be studied appear to be "banded," as if two very fast elements were connected by diffuse sound at diverse frequencies. This "two-parted" tendency suggests a basic aspect of the Yeh Call Complex, the composite nature of the notes with many calls or notes appearing double or triple. There is a resemblance of these Yik notes to Kyik Calls, but the former are much weaker, they lack any "tailing" of sound terminally, and there is no particular emphasis at the frequencies emphasized in Kyik Calls.

Yeh Notes (fig. 4B): These are weak, vertical notes 0.015 to 0.02 second in duration with sound continuously, or at many emphasized points between 0.8 and 3.0 kilohertz. Most sound is in the 1 to 2 kilohertz range. Points of emphasis differ from note to note. Wide band spectrographic analysis (sample of 20) shows that the notes are very fast, inverted, V-shaped, with peaks at intervals as close as 0.4 kilohertz. These notes are uttered in loose series, or in various combinations with other forms of Yeh Calls.

Yeh-yeh Call (fig. 4C): Single ("yeh"), double ("yeh-yeh"), or variant multiple notes comprise this call. Each note is composed of two elements, each 0.01 to 0.015 second in duration, spectrographically consisting of a vertical column from 0.9 to 2.6 kilohertz. The elements vary within each note, so the notes are irregular in appearance. A note is 0.035 to 0.04 second in duration. There is no connection between the vertical elements of a note. Some notes closely resemble the less formed, terminal notes of series of Tewk Calls of *Picoides villosus*, and a few notes are virtually identical in all respects. Tewk Calls of *P. pubescens* are less similar but a few variant notes show some resemblance to the Yeh-yeh Call of *arcticus*. Variant multiple notes considered part of this call may be related to the notes just discussed. These have three or four vertical elements—within 0.045 second (three elements) or

0.06 second (four elements). The elements vary within a note, hence they are irregular. Nevertheless points of emphasis tend to be found at 1.5 and 3.0 kilohertz, and to a lesser extent at 0.8, 2.3, and 4.8 kilohertz. These notes somewhat resemble Snarl Call (fig. 4G) notes, but the elements are uttered at a 50 percent faster rate, and are in small rather than large groups of five or more elements or notes.

Yeh-kk Call (fig. 4B, C, D): This call is given in series, often interspersed with Yeh notes and other calls of this complex. Notes of the Yeh-kk Call vary in number, consisting of an initial, typical Yeh note followed by one to four rapid ("kkkk") variable, but vertical notes. The yeh-k version of this call (18 examples) somewhat resembles the Yeh-Yeh Call, but is slower, and the "k" note differs from the initial "yeh" note in being longer, and often showing a banded form on a sonagram. The lead note also tends to be much weaker. These double calls also somewhat resemble the much stronger Kyik Call in having a weak, initial element. Notes vary from 0.03 to 0.085 second in duration, with a gap of 0.01 to 0.045 second between the two notes. There are three to five points of emphasis, at 0.8 to 1.3, at 1.5 to 2.5, at 3.3 to 3.9, and at 5.0 kilohertz and above. The initial note is weaker in every case, and points of emphasis always vary between notes of a call. Dominant frequencies are those between 1.0 and 2.6 kilohertz, but occasionally there is more emphasis at 3.3 or even 5.5 kilohertz. The three-noted yeh-kk version (fig. 4C; 30 examples) is 0.07 to 0.095 second in duration, the extra, fast "k" note adding little to the duration of the call. The gap between notes one and two is the same as in the two-noted version. The last note, or occasionally the last two or the second note, is strongest. The main emphasis tends to be between 1.6 and 2.6 kilohertz, but there are as many as six points emphasized between 0.8 and 3.6 kilohertz. Stronger notes tend to appear banded in wide band analysis. Four-noted calls of the yeh-kkk version (fig. 4B, D; 22 examples) are 0.095 to 0.12 second in duration, and otherwise resemble three-noted calls. One or the other or all the last three (kkk) notes are strongest. Finally, the five-noted, yeh-kkkk version (fig. 4B; four examples) lasts 0.12 to 0.13 second. Again, no two adjacent notes are alike in

their points of emphasis. Dominant frequencies are between 1.3 and 3.3 kilohertz.

Kkkk Series: In a few instances I recorded fast, soft series of "kkkk" notes, numbering three or four in a call. These essentially are Yeh-kk Calls lacking the yeh note. Their duration (e.g., 0.06 second for three notes, 0.085 second for four notes) and frequencies emphasized, as well as their form (variable note to note, vertical notes with emphasized points) entirely resemble the kk portion of a Yeh-kk Call, which see. These series were given amid series of other calls of the Yeh Complex.

Several examples indicate how these are used in relation to one another. Of course I could not be certain whether a single adult uttered the calls in sequence. One series of nine calls in 2.33 seconds varied in rate of delivery of the calls between three and five per second. The calls given were: yeh-k, yeh-kk, yeh-kk, yeh-kk, yeh-kk, yeh-kk, yeh-kk, yeh-kk, yeh-kkk. Another series of six calls in 1.83 second ($3\frac{1}{2}$ to 4 per second, average 3.6 calls per second) follows: yeh-kk, yeh-kkk, yeh-k, yeh-kk, yeh-kkk, yeh-kk. Still another series of 11 calls and notes in 1.88 second was: yeh, yeh, yeh-kk, yeh-k, yeh, yeh-k, yeh, yeh-k, yik, yeh-kk, kkkk. Finally, a fourth series of seven calls in 1.85 second (3.8 calls per second) was: yeh-kk, yeh-kk, yeh-kkk, yeh-kkkk, yeh-kkk, yeh-yeh, yeh-kk. All of these sequences are from longer, partly recorded series obtained during encounters of the male and female *arcticus* at the nest.

Comparable calls of *P. tridactylus* were not heard. Probably some calls cited in the literature of this species will prove related to the Yeh Complex. Among these may be the "Kri-Kri-Kri" or "Wätsch-Wätsch" mentioned by Scherzinger (1972, p. 207), or the "grügrügrügrü" or "chchchch" noted by Lanz (1950, p. 50), all reported from European *tridactylus*.

Kyik-ek Call

This distinctive call was recorded primarily from a nesting female Black-backed Three-toed Woodpecker, but I heard several such calls, and tape-recorded one from a male of that species. This was the predominant call of the female at the nest, Kyik-ek Call series being given on 92

visits by the female (out of 150 visits in which she was vocal). The male more frequently uttered Kyik Calls in the same circumstances, and only twice (of 97 visits in which he was vocal) did the male give a Kyik-ek series.

The variable Kyik-ek Call ordinarily was given in a series of up to four or five calls as the bird flew away from the nest. Naturally the later calls of a series diminished in volume as the bird flew away, and I recorded mainly the first two or three calls of any given series. I was able to record four examples of four-note calls, and analysis of these and comparison with two-call and three-call (i.e., initial two and three calls of a series) series shows that there generally is an increase in time between calls within a series as it progresses. Thus, there was an average of 0.88 second between calls one and two (12 examples), 0.98 second between two and three, and 1.16 second between three and four. One call series proved to be an exception, with diminishing times of 1.02, 0.98, and 0.71 second between its calls.

A call usually consists of two parts, an initial kyik note followed by a series of one to three ek notes (these versions are illustrated in fig. 4C, D, E, F). Some calls lack the kyik note (fig. 4D), but it was present in 34 of 58 calls analyzed. Infrequently the initial note is a weak yik note, instead of a fully formed Kyik (six instances). In 18 calls there was no kyik or yik introductory note (fig. 4D). The ek notes vary in number within a call, from one to three. Numbers of each were 16 with one note (fig. 4E), 25 with two notes (fig. 4C), and 15 with three notes (fig. 4D). Calls having both kyik and ek parts usually had one or two ek notes, whereas calls lacking a kyik (or yik) generally had two or three ek notes (15 of 16 one-noted ek-bearing calls had an initial kyik note, and 13 of 15 three-noted ek-bearing calls lacked a kyik note). The kyik and ek portions were analyzed in detail.

The kyik notes of the Kyik-ek Call (fig. 4C, D, E) generally resemble Kyik Calls closely, and the Kyik Call may be considered as incorporated into the Kyik-ek Call. The kyik in the Kyik-ek Calls perhaps more often than in the Kyik Call shows a weak to strong initial vertical element (see, e.g., fig. 4C) and less often shows an angling away from the vertical column. In one call the kyik has

a lead element stronger than the second element, giving a peculiar double note. This double-noted tendency is found in the Yeh Complex of calls as well. The duration of the kyik notes is 0.015 to 0.025, or rarely 0.03 second, without the lead element. The main emphasis is between 1.3 and 2.7 kilohertz, or occasionally 3.3 to 3.8 kilohertz in a few notes.

Ek notes of the Kyik-ek Call vary in the number of vertical elements contained. An ek note may be composed of from two to nine vertical elements, fast, irregular elements with points or more usually broader areas of sound at intervals, giving a characteristic waved, banded appearance on sonagrams. The main emphasis in these elements is at 0.8 to 3.6 kilohertz, with vague sound indicated above 4.0 kilohertz. A characteristic of these elements is their irregularity, no two adjacent ones being alike in their points of emphasis. Most ek notes have four to seven such elements (only nine of 125 have two, three, eight, or nine elements), and the average number per note is 5.41 elements. The tempo of the elements varies between 67 and 103 elements per second, with averages for notes with different numbers of elements all falling between 75 and 80 elements per second. I found no difference in these elements between ek notes in Kyik-ek Calls with (fig. 4C, D, E) and those in Kyik-ek Calls without (fig. 4D) a kyik note. No pattern was evident in the multiple ek notes of a given call, that is, there was neither a decrease nor increase in number of elements per ek note, nor was there a change in tempo of delivery of the elements in consecutive ek notes. The average duration of various ek notes with these numbers of elements were: two elements, 0.03 second (N=1); three elements, 0.036 second (N=6); four elements, 0.05 second (N=26); five elements, 0.065 second (N=43); six elements, 0.078 second (N=29); seven elements, 0.09 second (N=18); eight elements, 0.10 second (N=1); and nine elements, 0.12 second (N=1).

Gaps between ek notes varied from 0.02 to 0.045 second, and somewhat greater gaps (0.02 to 0.07 second) separated kyik notes from the following ek note. One peculiar yik-ek version of the Kyik-ek Call showed a gap of 0.15 second between the yik and the ek.

I could find no pattern of sequence in notes of various series of Kyik-ek Calls, except that

mixed series having calls with and calls without the initial kyik always began with a call having a kyik note. Some representative sequences are as follows, with K indicating kyik notes, Y the yik version of a kyik note, and numbers denoting the ek notes of the calls: K-2, K-2; K-2, K-3; K-3, K-3; K-2 (plus a terminal yik note, see fig. 4D), 3; K-1, 3; K-2, 2; K-2, 3, K-1, K-1; Y-3, 3; Y-2, Y-1, K-2, 2; 3, 2; and 3, 3.

Kyik-ek Calls somewhat resemble Yeh-kk Calls, but differ in the strong lead note (Kyik instead of yeh), and in having very rapid vertical elements arranged in discrete, often multiple (ek) notes, rather than lower, separate k notes. Also the banded appearance of ek notes in the Kyik-ek Call is a distinctive characteristic. This banding and the tight vertical elements resemble some screechlike distress calls of *Picoides pubescens* (fig. 3D).

On May 2, I tape-recorded a peculiar series of Kyik-ek-like calls (fig. 4F) from one of a pair of *arcticus* flying away from an encounter with a pair of *tridactylus*. The series contained eight notes (the first two are shown in fig. 4F), in sequence as follows: 1) a grating "tyaa-eeeh-eeek" (the e's short, not long); 2) a similar "tyeh-eeeh"; 3) a shorter "tyeh-eh"; 4) a still shorter "yik-eh"; 5) a "d-yeh"; 6) a "yik-ekk"; 7) a "yik-kkk"; and, 8) a Kyik Call. The ek-like notes of these calls are given at rates of 62 to 80 elements per second, as in ek notes of Kyik-ek Calls. However, the elements are not clear and distinct, but diffuse sound connects them, at 1.5 and especially at about 3.0 kilohertz, obscuring the elements on sonagrams, and giving them their rasping, or grating quality. The first seven calls of the series show this diffusion in their ek-like notes, although the later calls are clearer and their notes are more ek-like. Even these later notes, however, lack the usually wavering quality of the spectrographically banded elements of ek notes. The yik notes, where they are formed, are comparable to yik notes in the yik-ek version of the Kyik-ek Call. The initial two calls of this peculiar series show close resemblance to the screechlike distress call of *Picoides pubescens* (fig. 3D), but resemblance to the Screech Call of *arcticus* (fig. 3D, H) is less because the frequencies that are emphasized differ. Whether this screechy ek series of calls represents a distinct

call remains to be seen, and obviously more data are needed.

Kyik-ek Calls appear to be vocal threat displays of less intensity than Scream-Rattle-Snarl Calls. The reason for a preponderance of Kyik-ek Calls by females is unclear. It is certain that the call is used aggressively, as it clearly was directed at me on several occasions, at males by the female, and once by the female at a Tree Swallow (*Iridoprocne bicolor*) hovering near the Black-back's nest.

Kweek Call

Rendered "Queek" Call in Short, 1971, was heard several times from *P. tridactylus*, but it does not to my knowledge occur in *P. arcticus*. The call is a series of long kweek notes, and those heard sound much like Kweek Calls of *P. villosus* and *P. scalaris*. Unfortunately I was unable to tape-record this call. It is essential that the Kweek Call be studied in detail, as it will provide an insight into possibly derivative calls of *P. arcticus* (see Snarl-Rattle-Scream Complex below), as well as data for comparison with *villosus* and other congeneric species.

One Kweek Call was uttered by a female *tridactylus* simultaneously with a Scream-Rattle-Snarl Call of a female *arcticus* as the former bird attacked and supplanted the latter. Other Kweek Calls also were heard during encounters between *tridactylus* and *arcticus* (since *arcticus* never uttered such calls in numerous intraspecific conflicts, it is unlikely that Kweek Calls heard in the interspecific encounters were rendered by *arcticus*), in which *arcticus* uttered Kyik, Kyik-ek, and Scream-Rattle-Snarl calls.

Snarl-Rattle-Scream Complex

A functionally and structurally related array of calls forms this complex in *Picoides arcticus*. Calls include the Snarl Call, the Rattle-Snarl Call, the Rattle Call, the Scream-Rattle Call, and the Scream-Rattle-Snarl Call. Basically the snarl notes are fast, vertical notes, the rattle notes are slower, and scream notes differ from these, but invariably are uttered in combination with rattle, or with rattle and snarl notes. This complex seems unique to *P. arcticus*, and appears partly to replace the Kweek Call of related species, appar-

ently including *tridactylus*, which have a Rattle Call but lack the Scream and Snarl calls of *arcticus*. These calls are discussed in the order in which they occur alone and in combination in *arcticus*.

Snarl Call (fig. 4G): Very like the Fast Rattle Call (fig. 4A) of nestling Black-backed Three-toed Woodpeckers, and may be derived ontogenetically from it. Its pitch is lower and the sound is concentrated at fewer points than in the nestling Fast Rattle Call. Snarl Calls are variable in duration and in the number of notes contained, and they are mixed irregularly with Scream-Rattle-Snarl Calls and various Yeh Complex calls during confrontations between birds, either mates, other conspecific individuals, or birds of other species. Notes of the Snarl Call are delivered more rapidly than in the Rattle Call, and they are less loud.

Snarl Calls vary from 0.06 to 0.85 second in duration, having three to 32 notes ($N=40$). Seventeen Snarl Calls of less than 0.15 second in duration average 48.9 notes per second, whereas 23 calls longer than 0.15 second average slower, at 41.3 notes per second. The range in tempo is from 36 to 59 notes per call in 40 Snarl Calls. Hence the tempo of the notes is greater than in other calls of this complex, but even the fastest is less than the rate of delivery of elements in ek notes of Kyik-ek Calls. The average number of notes per call is 9.2

Sound is concentrated between 0.8 and 4.2 kilohertz, with the strongest emphasis most frequently at 1.5 to 2.1 kilohertz. Consecutive notes generally vary, such that an irregularity is imparted to the calls.

Five combinations of Rattle-Snarl Calls (fig. 4H) were available for analysis. These are mixed couplets, a Rattle immediately preceding a Snarl in each case. These compound calls permit a comparison of the two calls, which shows a tendency for Rattle Call notes to have a lower pitched (four of five cases) range of major emphasis. The initial Rattle Call contained eight to 13 notes, delivered in 0.25 to 0.42 second at a rate of 27.6 to 32.5 notes per second. After a gap of 0.02 to 0.06 second there followed a Snarl Call containing seven to 27 notes, lasting 0.17 to 0.64 second, with a rate of 39.6 to 47.0 notes per second.

Snarl Calls are commonly uttered, but would pass unnoticed by an observer most of the time because of their weakness and lack of carrying power if it were not for their association with louder Scream-Rattle Calls. The Snarl Call appears to be a low intensity aggressive call containing elements of threat and perhaps of submissiveness. To some extent it replaces the Kweek Calls of related species of *Picoides* (see Short, 1971).

Rattle Calls: Known for many species of *Picoides* (Short, 1970, 1971, 1973), these are threat displays of moderate intensity used during encounters and in territorial proclamation. The Rattle Calls usually are an elaboration of the species' call note, uttered in series. Both three-toed woodpeckers have a Rattle Call, but it is complexly woven into a framework of closely similar calls in *arcticus*, and hence is uncommonly heard by itself.

Five Rattle Calls of *P. tridactylus* (fig. 5B) were tape-recorded sufficiently well to permit analysis, and two of these were obtained during encounters between *tridactylus* and *arcticus*. Calls were 0.49 to 2.46 seconds in duration (average 1.1 seconds), and contained six to 26 notes (average 12 notes). Their tempo varied from 10.67 to 11.90 notes per second, averaging 11.08 notes per second. As in the Pik Call notes, which they resemble, the Rattle Call notes show a dominant fundamental tone and weak (one moderate) harmonic tones. Notes are inverted, U-shaped, with emphasis on the peak at 2.1 to 2.5 kilohertz, and a weak harmonic tone peak at 4.1 to 4.7 kilohertz. Their duration is 0.025 to 0.03 second. Some variation in frequency occurs in each call, but there seems to be no pattern of rising or falling. The tempo shows little change through a call, perhaps slowing slightly on the average. Longer calls tend to have a weak section, e.g., between notes 9 to 13 in the 26-note call.

The Rattle Call of *P. tridactylus* resembles that of *P. pubescens* (fig. 5C, G) in the general shape of the notes, their duration, and the average rate of delivery, but the pitch is much lower (peak of fundamental tone about 2.3 kilohertz in *tridactylus* versus 3.5 kilohertz in *pubescens*). Rattle Calls of *pubescens* show a shift in tempo from 11.3 to 14.0 notes per second during the call, an increase of 24 percent, thus differing from *tridactylus*. There is an even closer resem-

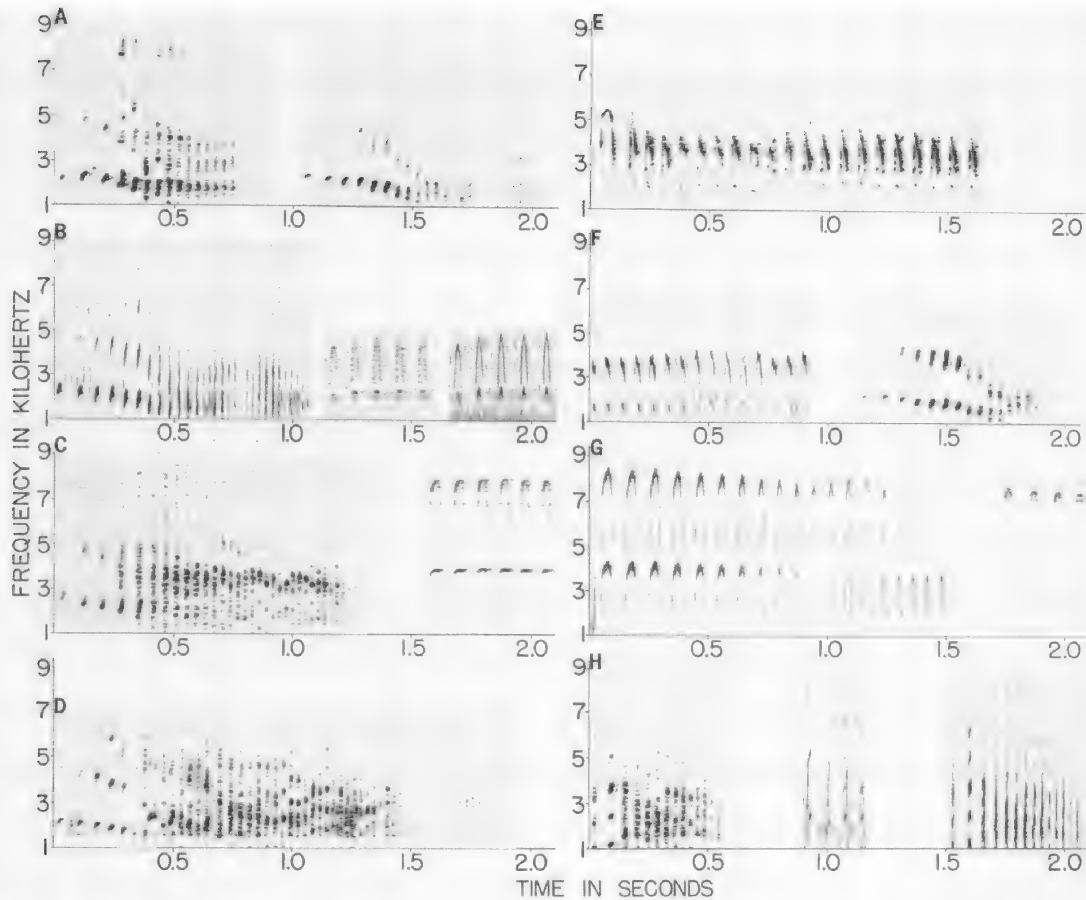


FIG. 5. Sound spectrograph of some calls of *Picoides arcticus*, *P. tridactylus*, *P. villosus*, and *P. pubescens*. A. Scream-Rattle Call of male *arcticus*, followed by Scream-Rattle-Snarl Call of either male or female *arcticus*. B. Scream-Rattle-Snarl Call of *arcticus* same as immediately preceding call in (A), but WB, followed by five notes from middle of a Rattle Call of *tridactylus*, then same notes, WB. C. Scream-Rattle-Snarl Call of *arcticus* (five scream notes, then nine rattle notes, then 20 snarl notes), followed by six notes from Rattle Call of *pubescens*. D. Scream-Rattle-Snarl Calls of displaying male and female *arcticus*, with initial scream notes of first call (notice Snarl Call of other bird in background at 0.1 second), then scream notes of second call commencing at 0.4 second; both calls then continue simultaneously, terminating in snarl notes of second call. E. Rattle Call of *villosus*, introduced by peek note. F. Part of Rattle Call, WB, of *villosus*, followed by Scream-Rattle Call of *arcticus* showing nine scream notes. G. Short-noted Rattle Call of *pubescens*, WB, version with equal emphasis on fundamental and initial harmonic tones, followed by four notes from another Short-noted Rattle Call, version with emphasis only on harmonic tone. H. Partial Scream-Rattle Call of female *arcticus* (note banded second note), followed by four notes, WB, of fledgling Tewk Call of *pubescens*, to be compared with banded second note of following Partial Scream-Rattle Call, WB (same call as previous, narrow band Partial Scream-Rattle). All sonagrams narrow band unless indicated wide band by WB, from recordings obtained in New York and adjacent New Jersey, mainly in Hamilton County, New York.

blance of the Rattle Calls of *tridactylus* and Asian *P. canicapillus* (Short, 1973, fig. 15d), and, indeed, except for the trifle slower delivery of *tridactylus*, calls of the two species are virtually identical. Rattle Calls of *P. villosus* (fig. 5E, F) are generally longer than those of *tridactylus*, the tempo is faster (14.62 notes per second), there is a slight decrease in tempo (7%) through the call, and, although the peak of the fundamental tone is about the same, that tone is much weaker than the dominant harmonic tone at 4 to 5 kilohertz.

Only two analyzable, simple Rattle Calls of *P. arcticus* were available (both with background sounds of nestlings), but additional data were available for Rattle Calls given in Rattle-Snarl Call (see, e.g., first part of fig. 4H) combinations, and of course from those in Scream-Rattle (fig. 5A) and Scream-Rattle-Snarl calls (e.g., fig. 5B). Thus, about 40 "rattles" form the basis for discussion. Notes of the calls are 0.01 to 0.015 second in duration, and appear on sonagrams as vertical columns with spots indicating concentrations of sound at various frequencies. In some cases there is an emphasis on a presumed fundamental tone at 1.5 to 2.0 kilohertz, with higher harmonic tones at appropriate intervals, whereas the emphasis is at scattered points in other calls. Calls contain six to 23 notes delivered in 0.23 to 0.77 second. The rate of delivery varies between 24 and 33 notes per second, with an average of 28 notes per second. The Rattle Call thus shows no overlap in tempo with the Snarl Call.

Compared with other species, *arcticus* has a Rattle Call faster than the fast Rattle Call of *P. nuttallii* (Short, 1971, pp. 85-86), and lower in pitch, with notes in a tighter inverted V such as to form a vertical column on a sonagram. In pitch the notes emphasize about the same frequencies as do notes of the slower Rattle Call of *P. villosus* (fig. 5E, F), but the notes are shorter and vertical, not inverted U-shaped.

Scream-Rattle and Scream-Rattle-Snarl Calls

Scream notes are loud, and invariably given in series as an introductory portion of various complex calls, mainly the Scream-Rattle Call (fig. 5A) and the Scream-Rattle-Snarl Call (figs. 4H, 5B, C, D, F). The notes of the Scream segment

are rattle-like (indeed, there are intermediate notes), but have more definite emphasis at various frequencies. Notes are generally vertical in form, but spectrographically, the initial notes of a series tend to be broad (horizontally) and later notes are more vertical with a definite rising tendency. The series show a strong drop in pitch of the notes, and a speedup through the scream part of a call.

Scream notes vary in duration (0.02 to 0.04 second) and pitch. Initial notes generally lack overtones, and often are very weak; their fundamental tone receives all emphasis at from 2.1 to 2.6 kilohertz. Subsequent notes generally drop in pitch and show stronger harmonic tones, but some, because of their more vertical aspect, have sound at the fundamental tone over $\frac{1}{2}$ to 1 kilohertz. Terminal scream notes are from 0.5 kilohertz to 1.0 kilohertz lower in frequency than the initial note, with the drop greater in longer series. The fundamental tone is dominant in most notes, but may be co-dominant with the initial harmonic tone in later notes of a series, in which other harmonic tones also are prominent. Later scream notes in a series increasingly come to resemble the following initial rattle notes, and are intermediate in some cases. Gaps between notes in a series diminish from 0.06 to 0.09 second between notes 1 and 2, to 0.03 to 0.06 second between the last two notes (the more notes in the scream the shorter the gaps between later notes).

Scream series contain two to 10 notes uttered in 0.09 to 0.59 second, with notes delivered at rates of 12.7 to 22.2 notes per second; respective means for 35 scream series are 5.34 notes per call, 0.333 second duration per call, and a rate of 16.42 notes per second. The rate of delivery is considerably less than in the Rattle Call, approximating the tempo of notes in Rattle Calls of *P. villosus* and *scalaris* (Short, 1971). However, scream notes do not resemble rattle notes of those species. Rather, there are resemblances to distress calls and some Tewk Calls of *P. pubescens* (see below).

Various calls containing scream series are considered individually in the following subsections.

Partial Scream-Rattle Calls: Four peculiar calls (fig. 5H) contained abbreviated screams, with few, often incompletely formed scream notes. A

12-note call of 0.48 second duration was introduced by a loud scream note with emphasis at 1.7 and 3.4 kilohertz. The other 11 notes form a typical rattle series, except that the first of them is banded, with emphasis at 1.8 kilohertz and above (the others are emphasized at 1.4 kilohertz and above), and tends toward a scream note. An eight-note call was introduced by two scream notes, followed by six typical rattle notes. A 16-note call commenced with an intermediate scream-rattle note. Finally, two intermediate notes began a half-second series of 14 notes (fig. 5H), the last 12 of which were rattle notes showing diffuse sound from 0.8 to 6.0 kilohertz with emphasis between 1.5 and 3.4 kilohertz. The initial two notes of this call show a screamlike drop in frequency, and they are loud. The first note is emphasized at 1.2, 2.4, 3.6 (dominant), 4.9, and 6.0 kilohertz, resembling some notes of *P. pubescens*, especially some fledgling tewk notes that are almost identical (fig. 5H).

Scream-Rattle Call: Eight analyzed calls contain scream and rattle series, but no snarl series. These calls (fig. 5A) are 0.38 to 1.07 seconds in duration and contain nine to 25 notes. From four to nine scream notes comprised 35 to 49 percent of the duration of these calls. Three calls are of special interest. One call of 22 notes has five scream notes, two intermediate scream-rattle notes, and 15 typical rattle notes. The intermediate notes have very discrete points of emphasis and are slightly skewed like terminal scream notes, but are at a lower pitch than those notes; they also are intermediate in loudness. A call of 12 notes has four initial scream notes that give way to peculiar rattle-like notes, having few concentrations of sound, and delivered at 17.8 notes per second. The tempo of these notes is that of a scream, not of a rattle. I cannot comment on this variation, except that it stresses the similarity of rattle and scream notes. A typical Scream-Rattle Call of 15 notes was uttered simultaneously with a Scream-Rattle-Snarl Call (see below), the two occurring during an encounter between a nesting female and an intruding strange male of *P. arcticus*. I could not establish which bird gave which call.

Scream-Rattle-Snarl Call: This call incorporates consecutively a scream series, a Rattle Call, and a Snarl Call into one composite call. Among

the calls recorded on tape are 13 recorded satisfactorily (figs. 4H, 5A, B, C, D, F), and eight others in which all details of the rattle and snarl portions are not clear. Calls were 0.94 to 1.50 second in duration, with the three portions variable in duration within the calls. Two to 10 scream notes, eight to 23 rattle notes, and seven to 21 snarl notes were included in these calls. Six long Scream-Rattle-Snarl Calls additional to those already discussed are 1.42 to 1.74 second in duration, and contain 39 to 49 notes. All three components, but especially the snarl portion, tend to be longer in these calls. Also, scream notes are delivered slowly, at a rate less than 15.4 notes per second, compared with most shorter Scream-Rattle-Snarl Calls.

The Scream-Rattle-Snarl Call apparently is the call of *arcticus* mentioned by Kilham (1966, p. 309) as "*pet-pet-wree-oo*" and "*kick-kick-wree-oo*," noted during intraspecific conflicts. I found that this call invariably is associated with a Hunched-Wing Spreading Display (see below) during conflicts. This compound display and the call were noted during 39 of 247 vocal occurrences in visits of the adult male and female *arcticus* feeding at the nest over five days in June. Of the 39 instances, 23 were by the female and 16 by the male. Most calls were directed at each other, or at another intruding *arcticus*. Several were directed at me by the female, and the male used a Scream-Rattle-Snarl against a Tree Swallow (*Iridoprocne bicolor*). A few other instances might be noted. A female uttered a Scream-Rattle-Snarl Call, following a Rattle Call, as she supplanted a male at a nest he had been excavating. On May 3, a male *arcticus* attacked and supplanted a female *tridactylus*, employing the Hunched-Wing Spreading Display and Scream-Rattle-Snarl Call. A female *arcticus* responded to Rattle Calls of a male and female *tridactylus* on May 4 with Wing-Spreading and the Scream-Rattle-Snarl Call. At the nest on June 14, the male *arcticus* displayed and gave a Scream-Rattle-Snarl Call at the incoming female, which responded similarly as she landed, at which the male gave a Kyik Call, and left. Various calls of the Snarl-Rattle-Scream Complex thus seem to occur in situations involving Rattle and Kweek calls in other species of *Picoides*. The Snarl-Rattle-Scream Complex seems homologous to the Rat-

tle Call of the other species. There is no Kweek Call derivative in the vocal repertoire of *arcticus*, but Kweek and Rattle calls are structurally closely related, and it is possible that the Kweek Call, present in *P. tridactylus*, has been suppressed in *arcticus*, in favor of an elaborated Rattle Call, the Snarl-Rattle-Scream Complex.

VISUAL SIGNALS

Observations of displays in the North American three-toed woodpeckers are not numerous, and this discussion attempts only a preliminary categorization. Doubtless other displays remain to be discovered, and certainly further data are needed for those that are described below. The basis for this discussion has been provided in an earlier report on displays of other species of *Picoides* (Short, 1971, p. 71; see also Short, 1970, 1972, 1973). Most observations of the three-toed woodpecker displays were fragmentary, as birds often flew off together during continuing encounters, and many display sequences and the displays themselves transpired rapidly, hindering observation of details. Aggressive encounters between the mated pair of *P. arcticus*, which provided many observations of displays, tended to be brief (the pre-nesting phase, presumably involving more prolonged encounters and displays related to pair-formation, had concluded before my observations began), and perhaps the displays were abbreviated or partial, and their rapidity discouraged appreciation of all their nuances. Sequences of displays during encounters are presented in the section following this one, the task at hand being a description of the displays.

Bill Positioning Postures

Bill Directing (threat display) and Bill Raised postures (less threat, greater likelihood of fleeing perhaps indicated; see Short, 1971, p. 72) were noted in *P. arcticus*, and the Bill Directing Posture was seen in *tridactylus*. Bill Directing involves the lowering of the head and bill, and pointing the bill at an antagonist. A female *tridactylus* employed Bill Directing at a female *arcticus* before supplanting it, and the *arcticus* female used the same display against the *tridac-*

tylus female during the same encounter. Most episodes of Bill Directing were subtle, involving the mated pair of *arcticus*. The Bill Raised Posture was observed several times in *arcticus*, in each case used by a bird that fled moments later. This display consists of holding the head and bill high in the air, at up to a 90-degree angle. It probably occurs as such in *tridactylus*, for this posture is illustrated by Ruge (1968, p. 120, fig. 8b), but as a part of the Head Swinging Display in which it is incorporated.

A Bill Lowered Posture is the holding down of the bill and head, exposing the crown (the crest may be raised, see Crest Raising). The bill usually is held to one side, rather than toward the antagonist, perhaps relating to the Head Turned Posture of related species (Short, 1971, p. 72) that was not seen in the three-toed woodpeckers. I have seen the bill lowered in *P. villosus*, but not apparently ritualized to the extent noted in *P. arcticus*. The display often accompanies a Hunched Posture (see below) with fluffed plumage, usually in the subordinate bird in an encounter, or in response to a Wing Spreading Display. Two instances of the Bill Lowered Posture were observed in *tridactylus*, both by a female in response to displays of a female *arcticus*. The posture seemed less ritualized, and was accompanied by less or no "hunching," compared with that of *arcticus*.

Hunched Posture

The Hunched Posture involves the raised back so that it is curved in silhouette, and a lowered neck—the head and bill often are low in an accompanying Bill Lowered Posture, described above. The Hunched and Bill Lowered postures most often are seen in conjunction with the Wing Spreading Display and Scream-Rattle-Snarl Calls, forming a complex, multiple display. Occasionally the Hunched Posture is seen by itself in a submissive bird during an encounter. I judge it to be an appeasement or submissive agonistic display, and in the compound display involving Wing Spreading, it balances the strong threat aspect of the spread and flailing wings. I observed or glimpsed the Hunched Posture about 45 times in *arcticus*, in conjunction with other displays.

Although I saw apparently subordinate Northern Three-toed Woodpeckers with fluffed plumage and a somewhat "slouched" posture, I did not observe a distinctly "hunched" posture in that species.

Crest Raising Display

Crest Raising Displays were frequently seen, with about 55 observations in *arcticus* and at least seven instances in *tridactylus*. The position of the yellow patch on the crown of males causes the erecting of the feathers to present the patch forward, and the display might be termed a "Crest Forward Display." In *arcticus* the male maintained a partly erect, or fully erect crest whenever the female was nearby, and generally during encounters. Several times I could see that the female also displayed her crest accompanying or following the Scream-Rattle-Snarl Call.

Crest Raising seems to be a threat display, and it also clearly advertises the sex of the displayer. It is noteworthy that juvenile birds of both sexes have the yellow crown patch of the male. This patch is visible in nestlings with their heads at the nest entrance waiting to be fed. Thus, the adult female, perhaps intimidated by Crest Raising Displays of males, encounters male crown markings each time she feeds, and the adult male too encounters these blatant male markings when it feeds the young. There is a possibility that these, and other male-appearing markings of nestling woodpeckers (e.g., *Colaptes auratus*) lessen aggression in the parents, which perhaps might be expected to act aggressively toward the head-on "assault" (bill forward, resembling Bill Directing Posture) by the nestlings.

Crest Raising by *tridactylus* was seen during encounters with *arcticus*. The display, illustrated by Ruge (1968, fig. 8a) in European *tridactylus*, seems very like that of related species of *Picoides* (*arcticus*, and *scalaris*, *nuttallii*, *pubescens*, and *villosus*, Short, 1971; also *canicapillus*, *macei*, *darjellensis*, Short, 1973, and *major*, Short, unpublished data). However, I have not seen *tridactylus*, or other species of *Picoides*, use the Crest Raising Display in conjunction with so definite a hunching of the back (Hunched Posture) and lowering of the head (Bill Lowered Posture) as does *arcticus*.

Head Bobbing Display

This display is a ritualized movement of the head and bill, with alternation between the Bill Directing and Bill Raised postures (Short, 1971, p. 76). I have observed this display in *Picoides scalaris*, *P. nuttallii*, and *P. villosus*, but not in other species, nor did I see it in *arcticus* or *tridactylus*. It is not a prominent display in those *Picoides* in which it has been seen, and is best studied with use of motion picture photography. Hence its "absence" in the three-toed woodpeckers simply may reflect a dearth of appropriate studies. The Head Turning Display (Short, 1971, p. 77) is another rarely seen display, noted thus far only in *Picoides scalaris* and *P. nuttallii*, and not observed in *arcticus* or *tridactylus*—however, a hint of its occurrence in the latter is suggested by figures showing a strong head turning component of the Head Swinging Display of *tridactylus* in Ruge's report (1968, figs. 8c and d). As in the case of Head Bobbing Displays, Head Turning Displays best can be detected and studied through use of motion picture photography.

Head Swinging Display

Displays involving the side-to-side swinging of the bill and head, and often of the body, are characteristic of many woodpeckers (Short, 1970, 1971, 1972, 1973). The display adds a movement to the Head Turned Posture (where present) and the Bill Directing Posture, and in some instances also the Head Raised Posture. Called *Kopfschwenken* (Scherzinger, 1972, p. 208) or *Kopfpendeln* (Ruge, 1968, p. 119) in *Picoides tridactylus*, and "bill-waving" (Kilham, 1966, p. 309) in *P. arcticus*, Head Swinging Displays were observed in both three-toed woodpeckers. In *tridactylus* Head Swinging is more conspicuous, and seems to occur less often with Wing Spreading than in *arcticus*. On most occasions Head Swinging of *arcticus* passes unnoticed because of the more conspicuous Wing Spreading with which it usually is associated.

Two instances of Head Swinging unaccompanied by Wing Spreading were directed at nestlings during feeding by the adult female *arcticus*. The bill was directed forward, and the head swung in a narrow arc from side to side two or

three times in each case. In other instances it is closely associated with Wing Spreading, and most often is evident in the zigzag movement of an attacking, Wing Spreading bird as it advances toward its antagonist. The attacker sidles forward, swinging its head first to one side, then the other, maintaining and adjusting its spread wings.

Nine Head Swinging Displays of *P. tridactylus* were observed both with and without Wing Spreading Displays, and were similar in form to those of *arcticus*. In five cases Wing Spreading accompanied Head Swinging, but in four instances the latter display occurred alone, or with a Crest Raising Display. Generally the head was held rather high as it was swung widely from side to side, perhaps a reflection of intimidation by the larger *arcticus*. All Head Swinging Displays were seen during encounters with *arcticus*.

I could not associate definite calls with Head Swinging, which usually is accompanied by Tewk or Wicka calls in other species (Short, 1971). In fact the suppression of the Tewk Call in at least *arcticus* may be related to the general incorporation of Head Swinging Displays into a composite display with Wing Spreading, and concomitant evolution of a new, correlated vocalization, the Scream-Rattle-Snarl. A Rattle Call accompanied three Head Swinging incidents in *tridactylus*.

Wing Spreading Display

More frequent than similar displays in other species of *Picoides*, the Wing Spreading Display easily is the most conspicuous display of the three-toed woodpeckers. Rather than restricted to more intense, uncommon encounters, Wing Spreading occurs as well in many moderately intense encounters, especially in *P. arcticus*. Ritualized into a compound display with incorporation of the Hunched Posture, Crest Raising, Lowered Bill Posture, and sometimes Head Swinging, it is given with an accompanying Scream-Rattle-Snarl Call. The displaying bird may face its antagonist, or may turn sideward while using this composite display. In simpler form the display is seen with modified Head Swinging in a zigzagging Supplanting Attack exactly comparable with that of *P. nuttallii* (Short, 1971, fig. 20G; see also I),

and other species of *Picoides* (e.g., *P. macei*, Short, 1973).

The Wing Spreading Display of *tridactylus* seems to be associated less often with a less ritualized "hunching" of the body, and is associated with no special vocalization. Either Pik, Kweek, or Rattle calls may be uttered simultaneously with the display. Wing Spreading during conflicts resembles that of *P. scalaris* and *nuttallii* depicted by Short (1971, fig. 20A; for *tridactylus* see also Ruge, 1968, fig. 8C, D). The spread wings either are held or flailed at the antagonist, actually buffeting him at close range.

There is some variation in the extent of Wing Spreading, and this seems correlated with the intensity of the conflict and the completeness of the Scream-Rattle-Snarl Call in *arcticus*. A Scream-Rattle, or short Scream-Rattle-Snarl was given with the wings spread only partway (wing flicking, Short, 1971, p. 78). On the other hand I watched at close range a female displaying at me with a complete Hunched Posture and Wings Spread fully; as it uttered a long Scream-Rattle-Snarl I saw its wings waved, still fully stretched, at the beginning of each stage of the call, giving three noticeable jerks.

Wing Spreading Displays of the three-toed woodpeckers are threat displays, emphasizing aggressive movement toward an antagonist. In combination with a Hunched Posture or Head Swinging, the threat aspect is lessened, and an appeasement aspect thus is imparted to the overall display. In other species of *Picoides* (*villosus*, *scalaris*, *nuttallii*) a Kweek Call often accompanies Wing Spreading Displays (Short, 1971, p. 78), and this sometimes occurs in *tridactylus*, but the Scream-Rattle-Snarl Call has replaced the Kweek Call in *arcticus*. Within *Picoides*, Wing Spreading Displays also have been seen in *P. pubescens* (Kilham, 1962) and *P. borealis* (Ligon, 1970), in various European species (e.g., *P. major*, Blume, 1958; *P. minor*, Winkler, 1971, fig. 1), and in at least one Asian species (*P. macei*, Short, 1973). Used both intraspecifically and interspecifically, Wing Spreading Displays emphasize the usually barred wings (even "zebra"-striped, see *nuttallii* illustrated by Short, 1971, fig. 20G, and *macei* in Short, 1973, fig. 18), and the threat implied is obvious even to unrelated species such as Tree Swallows, and man.

Flutter Aerial Display

Essentially an aerial form of Wing Spreading Display (Short, 1971, p. 78), the Flutter Aerial Display involves a flight during which the wings are momentarily and periodically held in a fully spread (displaying wing pattern) or downward position. The overall effect is a mothlike, wavering flight with stilted wing movements, rendering the bird highly conspicuous. The Flutter Aerial Display at an antagonist becomes a Supplanting Attack, although the momentum of the flying bird does not automatically give it an advantage (see Short, 1971, p. 79). Similar flight displays, perhaps emphasizing a different wing movement, may be directed to one side, that is, it may be a "showy" flight across the path of an antagonist or mate. It frequently is employed by a male, or more usually female, apparently to incite its mate or to stimulate one or both antagonists in an encounter, when its mate is actively in conflict with an intruding bird. The bird giving the Flutter Aerial Display in such situations "buzzes" by the antagonists, often very close to them, after which the encounter proceeds more vigorously.

The Flutter Aerial Display is known in *Picoides scalaris*, *nuttallii*, *villosus*, *pubescens* (Short, 1971, pp. 78-79), *macei* (Short, 1973), *major*, *syriacus*, *medius*, and *minor* (Short, personal observ.), as well as *arcticus* and *tridactylus*. It undoubtedly differs somewhat among these species, and there may be other, similar aerial displays that have not been distinguished as yet from the Flutter Aerial Display. Motion pictures of these flight displays, which are difficult to obtain, are needed to permit elucidation of the details concerning these displays, and, eventually, interspecific comparisons.

The nesting female *arcticus* frequently employed the Flutter Aerial Display in flying to the nest when the male was present at the nest site. Usually the female supplanted her mate in this way. This display also was used in chases between these paired birds. I also saw the display by a male *arcticus* flying to a tree occupied by a female *tridactylus*. Conversely, the only observation of the full Flutter Aerial Display by *tridactylus* was of a female *tridactylus* employing it in a flight to the nesting tree of the *arcticus* pair; at

the time (May 3) the female *arcticus* was excavating at the nest site. This display otherwise was used interspecifically by closely related *P. scalaris* and *P. nuttallii* (Short, 1971, p. 93).

In species of *Picoides* other than the three-toeds, a Kweek Call ordinarily accompanies the Flutter Aerial Display (Short, 1971), and it may do so in *tridactylus*. I heard a Kweek Call from a flying *tridactylus* female during an encounter with a female *arcticus*, but was not close enough to note the flight characteristics, although the *tridactylus* flew noticeably slowly. Another, definitely Flutter Aerial displaying *tridactylus*, mentioned above, gave the Pik Call as it displayed. Flutter Aerial displaying *arcticus* uttered Snarl Calls, various Yeh Complex calls, and Scream-Rattle-Snarl Calls, and they often went into a Wing Spreading Display with a Scream-Rattle-Snarl Call as they landed.

Tail Spreading Display

Another widespread display in *Picoides* (and other woodpeckers, see Short, 1972) is the spreading of the tail feathers, sometimes accompanied by physical movement of the body and tail serving to expose the tail surface to an antagonist. It is an agonistic display indicating a tendency to flee or to appease, as well as to attack (Short, 1971, p. 79). Often the tail is spread throughout a conflict, with frequent shifts in the extent of spreading. Thus, an observer, having noted the spread tail, may find it difficult to pay attention to subsequent, often subtle shifts in tail spreading, and these may pass unnoticed as the observer concentrates on Wing Spreading or other more conspicuous aspects of an encounter. Tail Spreading Displays disclose to an antagonist the white and black barred outer rectrices of *arcticus* and *tridactylus*, and most other species in which they occur.

I did not observe many Tail Spreading Displays by *tridactylus*, which may or may not be significant. An attacking female *tridactylus* had the tail partly spread (two instances), and a fleeing *tridactylus* noticeably spread its tail. In *arcticus*, however, Tail Spreading was seen frequently. One instance clearly indicates the association of

Tail Spreading with a tendency to flee. A female *arcticus*, having attacked and supplanted a male *tridactylus*, had its tail partly spread; the *tridactylus* male then attacked the *arcticus* female—as she was supplanted her tail spread fully and she fled with it so spread. From her new position, the female *arcticus* then resumed her attack, closing her tail partly as she lunged upward at the male *tridactylus*. At times both birds in a conflict used approximately equal Tail Spreading Displays, as by a male and female *arcticus* with the female flying in to the nest, supplanting the male.

There seemed to be some association of the Tail Spreading Display with Flutter Aerial Displays, particularly by *arcticus* not flying to the attack, but displaying as they fly across the path of a mate or possible antagonist, or engaging in “inciting” Flutter Aerial Displays as discussed above.

Attacks

Usually of the supplanting type, attacks involve direct movement by hopping toward or flying at and supplanting an antagonist (see Short, 1971, p. 80). About half of approximately 42 attacks that were observed (this number includes four or five separate attacks in single, extended conflicts) in *arcticus* and *tridactylus* were supplanting attacks involving the flying (often in Flutter Aerial Display) at an antagonist and driving it from its position. The others involved lunging at an antagonist, the movements afoot. Some of the various displays accompanying attacks are mentioned above, and others are described below in the discussion of encounters. Attacks are accompanied by a sleeked plumage. Ordinarily they do not involve physical contact, but there is occasional buffeting of the wings, and infrequently a flying, supplanting attack involves the hitting and contact of two birds. On three occasions two birds actually clasped feet after such an attack, and fell grappling, twice all the way to the ground. Interestingly, two of these three cases were interspecific encounters, one between a female *arcticus* and a female *tridactylus*, the other between a female *arcticus* and a male *villosus*, and the third involved two males of *arcticus*.

Fleeing

A fleeing bird (see Short, 1971, p. 80) either flew or hopped away. Sometimes it offered resistance or displayed, using a partial Wing Spreading or Tail Spreading display. Often during encounters a fleeing bird returned to the attack. In one case a supplanted male *tridactylus*, caused to fly, simply did so in a tight circle and returned to drop down upon and supplant the female *arcticus* that had caused it to flee.

INTRASPECIFIC AND INTERSPECIFIC ENCOUNTERS

I observed encounters ranging from almost imperceptible “reactions” of one bird to another’s presence nearby, to repeated and violent conflicts. About 50 moderately intense to intense encounters were noted intraspecifically in *P. arcticus*, about 10 between *arcticus* and *tridactylus* (no intraspecific encounters of *tridactylus* were noted), and I saw 11 such conflicts between *arcticus* and various other avian species. There were also approximately 20 aggressive actions involving vocal and visual displays by *arcticus* directed at me. Several hundred additional “encounters” of lesser intensity were noticed and provided some data, but many occurred so rapidly that I am unable to describe them fully. Few display sequences, indeed perhaps none, were documented fully, for synchronous motion pictures, tape-recording and observations, plus the birds’ cooperation in staying within a reasonable distance and in full view of the observer, are requisites for complete documentation of events transpiring during an encounter. Thus, the following discussion presents overviews of the conspicuous events during some well-observed sequences.

Unisexual Encounters of Black-backs

I was able to observe only three encounters between Black-backed Woodpeckers of the same sex. Other encounters occurred, but I saw only one bird during or following the encounters, and hence was not able to appreciate the actual events of the conflict. I was surprised to find that, although other *arcticus* were seen during the time of nest excavation of the pair studied in

detail, there were no transgressions or conflicts involving other conspecific birds, but only *tri-dactylus*; in contrast, during the June nesting period when woodpeckers might be expected to be occupied at their own nests, there occurred all three conspecific unisexual conflicts of *arcticus*, all near the nest site.

On the afternoon of June 12 I spied a male Black-back (bird B) on a stub 70 meters west of the Black-back nest. Suddenly a second male (bird A) appeared in flight toward the nest, then veered sharply toward male B. Male A, which was the nesting male, flew at male B (possibly in Flutter Aerial Display), uttering a Scream-Rattle-Snarl Call, and landed, supplanting male B. As it landed, male A gave another Scream-Rattle-Snarl Call, hunching, but not lowering its bill, and raising its crest, and spreading its wings. Male B reacted by moving away, in Hunched Posture, with the bill lowered, looking much like a submissive *P. villosus*. The action proceeded about the back side of the tree, and then one bird dove into the undergrowth, followed shortly thereafter by the other. A few minutes later, a male that proved to be male B flew directly to the nest site. Male A flew in directly at male B, which dropped away from the nest and flew to a nearby stub, pursued by male A. The two birds perched a half-meter apart, with crown feathers erect and tails partly spread. Male A then drummed, and male B immediately flew away, far to the north.

Probably the same males were in conflict on the morning of June 14. Male A was at the nest site when a strange male, again designated male B, flew in to a tree 10 meters from the nest. Male A immediately flew at him with crest raised, hammering with his wings, driving male B from the tree, and then pursuing male B to a small stub. There both perched motionless, crests partly raised, on opposite sides of the 10-cm. thick trunk. After the pause, male B dropped off and flew away with male A pursuing him closely. These actions were so rapid that I did not notice the tail position or changes in crown feather erection.

At 06:44 on June 15 I was watching the *arcticus* nest, just entered by the male, when the female flew in and gave a Scream-Rattle-Snarl Call and Wing Spreading Display. The male came out of the nest, and both then displayed and

called. I chose to play back to them their Scream-Rattle-Snarl calls. The female flew off a short distance, while the male responded by drumming three or four times. Suddenly I heard a Scream-Rattle-Snarl Call in the direction of the female, and then in from that direction came a second male, called male B once again. Male B perched on the stub at which male A had drummed, below male A, and gave a Scream-Rattle-Snarl Call and Head Swinging and Wing Spreading displays. Male A moved upward to the tip of the stub. Both males then drummed, after which male B flew away to the southeast. Male A drummed several more times about the nest site, then flew off.

Bisexual Encounters of Black-backs

The nesting male and female *arcticus* frequently interacted, usually in weak to moderately intense encounters. I saw about 33 moderately intense to very intense encounters, the latter involving mutual displays and often supplanting attacks, during my observations at the nest on June 11 to 15. About a dozen such encounters were seen in late April and early May. Some of the encounters have strong reproductive overtones, which will be evident from some examples.

On April 26 the nesting pair, male and female, were perched in separate trees near the nest, whose construction had barely commenced. The female flew, apparently normally, away from the nest; the male immediately left in pursuit of the female, using a Flutter Aerial Display, with tail spread, and calling (low Yeh-k Calls). His pursuit brought him near the female, but he kept up the display beside her or to her rear, rather than actually flying at her. I saw no difference between his flight and other, more obviously aggressive Flutter Aerial Displays.

On several occasions the male was excavating the nesting cavity, when the female flew in, usually calling kyik. The male responded by flying either to a nearby stub, or farther away, but I noticed his fully spread tail on these occasions. These events resulted effectively in the supplanting of the male by the female, which then either "inspected" the excavating, or indulged in that activity for awhile.

The female flew up from feeding in low dead trees on May 1 and the male suddenly appeared, apparently pursuing her. As the female landed on a branch, she pivoted, perched crosswise, and uttered a fast series of kyik and yik notes. As she crouched, the male, which had landed about $\frac{1}{2}$ meter away, proceeded toward her, stopped to deliver a low drum, then, with crest partly erect, mounted from the side and rear. Copulation was incomplete, as the male seemed to slide sideways, off the female, somewhat prematurely. Both birds gave a post-copulatory series of Kyik Calls mixed with various calls of the Yeh Complex. Later that day the male drummed near the nest, and the female then appeared, tail spreading, and in a weak Flutter Aerial Display, calling "yik, yik" (perhaps with yeh notes as well), and supplanting the male. After peering into the nest briefly, she flew to a nearby perch; the male joined her there, and I heard a soft Rattle Call, then a Scream-Rattle-Snarl by the male as he half spread his wings and swung his head from side to side. Both flew off after that. On several other occasions the female supplanted the male, "inspected" the nest, then preened nearby as the male returned to excavate anew.

Other interactions occurred in June when the two adults happened to meet as they brought food to the young. On June 11 and 12 the feeding male on six different occasions ceased feeding, even though apparently not finished, when the female appeared to feed the young. The female then supplanted the male. Twice the male waited for the female to finish, then went back to complete his feeding. In at least one case the male definitely swallowed the food as he was supplanted, then flew off. Later in the week, however, I twice saw the male supplant the female, feed the young, and fly, then the female returned to the nest to resume and complete her feeding of the nestlings.

Early on June 13 both adults appeared at the nest, and the female gave the full Scream-Rattle-Snarl Call with Wing Spreading. The male, perched close to her, responded almost simultaneously with the same displays, but Wing Spreading to a lesser extent; he also swung his head perceptibly, then called (yeh notes, Yeh-kk Call), or perhaps both called as their bills touched. The female then fed the young, fol-

lowed by the male. On June 14 the female was feeding when the male arrived at the nest. The female greeted him with both wings held stretched, hunching her body and lowering her head so that the bill was pointing far downward, then screamed (Scream-Rattle-Snarl Call); the male responded with the same displays, his bill also lowered, but adding distinct forward Crest Raising so that the crown patch was conspicuous. The male then fed the young with the female perched only centimeters away. As the male ceased feeding, he pivoted, and gave a full Wing Spreading-scream combination, with the head not lowered so far; the female fled to a nearby stub. During the displays before the male had fed his bill could be seen to hold many prey items, some of which were dropped in the antics of his displaying.

Later, on June 14 I was watching near the nest when the male flew to it, fed, entered the nest, exited carrying a fecal sac, and flew to a nearby stub. He tossed away the sac, drummed, then flew to a thin stub 2 meters from my face. Suddenly I saw his crest rise, and turning in the direction in which he was looking, I spied the female, still far off. As she approached to within 20 or 30 meters, the male hunched, spread his wings, lowered his head and bill, and screamed ("scream" used alone refers to a full Scream-Rattle-Snarl Call), directing his erected crest forward in the direction of the female. The female landed near the nest, carrying food, and screamed and spread her wings in response to the male. After several Kyik Calls, the male flew away, and the female fed the young.

Both adults arrived together at 08:31 on June 15, the male in full Flutter Aerial Display. Landing at the nest, they simultaneously screamed and spread their wings, then, both in Hunched Posture and with crown feathers erected, the male called kyik and the female gave Snarl Calls and Yeh-kk Calls. The male fed the young as the female waited beside the nest then fed the young when the male left.

Various of these displays, which basically are aggressive, show aspects relating to pair formation. There is for example a frequent coupling of Crest Raising with a Lowered Bill Posture by both birds, but especially the male. This is in contrast to Crest Raising with Bill Directing

(toward an antagonist) seen in unisexual encounters, and in the nesting male that has spied a distant woodpecker in flight, prior to "identifying" it as its mate. Nevertheless, most of the displaying during encounters between these obviously paired birds was aggressive in nature. Kilham (1966, pp. 309-310) also noted the strong aggressiveness of paired Black-backs. I have elsewhere discussed (1971, p. 102) the influence of agonistic behavior on pair formation. One might expect that such aggressiveness would diminish greatly after the pair has been formed, and indeed it may in some pairs of *arcticus* (Kilham, 1966, mentioned variation in aggressiveness among pairs). The frequent interspecific encounters of the *arcticus* pair with other avian species (see below) suggests that the relatively exposed situation of the nest site, and competition among several species for such sites, may be factors promoting aggressiveness in these woodpeckers.

Encounters Between Black-backs and Northerns

Some of the more intense encounters observed were between *arcticus* and *tridactylus*, and in fact most of the information about displays of the latter species is drawn from observations of such conflicts. Eight major conflict situations were observed partly or entirely, and these involved 17 instances of attacks or chases. All of these occurred between April 26 and May 4. Encounters between these two closely related species otherwise have been mentioned only by Gibbon (1966, p. 226, one "combat" between a male *arcticus* and a male *tridactylus*).

On April 26 a pair of *tridactylus* perched in adjacent stubs, and the male drummed. In flew a male *arcticus*; the *tridactylus* female flew, and the male *tridactylus* remained momentarily, then fled as it was supplanted by the attacking *arcticus*. The *arcticus* male then chased after the male *tridactylus*.

Several drumming bouts, not included as encounters of an intense nature, involved the nesting male *arcticus* on April 26 and 30. In these cases a *tridactylus* of unknown sex perched in a stub about 100 meters west of the nest, and drummed. The male *arcticus* ceased excavating

immediately, and drummed loudly. A drumming exchange of two or three bursts occurred, and then in each case the *tridactylus* flew away. Another bout largely involving drumming occurred on May 1. A female *tridactylus* foraging in a tall stub suddenly was supplanted by an incoming *arcticus* male. The latter then drummed several times. The female *tridactylus* perched in a dense spruce tree nearby as he drummed, but then flew away.

I missed most of a conflict from which emanated Kweek, Kyik, and Scream-Rattle-Snarl calls on May 2. This proved to have involved a male *tridactylus* and a pair of *arcticus*. The *tridactylus* apparently had been attacked and driven into a dense tree; the *arcticus* pair flew off, one bird uttering a Rattle Call and Snarl Call.

Early on May 3, I was near the *arcticus* nest in which the male was excavating when a female *tridactylus* landed in a tree beside the nest, and drummed. Out stormed the *arcticus* male in a Flutter Aerial Display to the attack, landing, and supplanting the female *tridactylus* by Wing Spreading and giving a Scream-Rattle-Snarl Call. The *tridactylus* sped away.

Later the same day the female *arcticus* (FA) was excavating in its nest. A female *tridactylus* (FT) probably the same bird as earlier in the morning, flew to the stub near the nest and drummed; it then called pik, and then, in a Flutter Aerial Display seemingly identical with that of *arcticus*, flew to the *arcticus* nest site. Out burst FA, attacking directly, and supplanting FT, which had gone into a Bill Lowered Posture as FA approached. Then FT fled, called "pik-ik-ik-ik" (Rattle Call), and landed nearby. FA flew directly to FT, and dropped on it, Wing Spreading as FT spread its wings and swung its head. Both birds, feet clasped, fell tumbling to the ground. There was a pause during which I could see no birds. Both then appeared, Rattling, in a chase. They perched in a tree 100 meters from the nest. FA attacked FT, using a Wing Spreading Display (and probably screaming) in its approach, with plumage sleeked, and perhaps Head Swinging slightly. FT responded with Wing Spreading and Head Swinging displays. Suddenly a male *tridactylus* (MT) flew in to the same thin stub, landing below the two females. FT immediately moved upward on the stub, becoming qui-

escent near its top. MT moved opposite FA on the stub, and FA responded with Bill Directing, Wing Spreading, and a lunging attack on MT, which responded with a Wing Spreading Display (probably Head Swinging also). MT nevertheless was supplanted by FA, then dropped off the stub, flew out in a small circle, and back at FA, dropping upon and supplanting her in turn. As FA backed downward from MT, she spread her tail fully. Then, plumage sleeked, FA thrust forward her bill, and with tail now half spread, lunged upward at MT, which, head swinging weakly, gave way and moved upward, thus being supplanted. Action ceased momentarily, then MT flew off to the south. FA, "ignoring" quiescent FT, then flew partway toward its nest, but stopped in a stub short of the nest. FT flew after FA, perhaps in partial Flutter Aerial Display, and landed, launching an attack with a Wing Spreading Display; she succeeded in supplanting FA, but both battled, Wing Spreading, Rattling, and giving other calls not fully heard—there was then a chase to the southwest, FA apparently pursuing FT.

A male *tridactylus* appeared near the *arcticus* nest on May 4, and drummed several times in a stub beside the nest. The *arcticus* pair were away, and no interaction ensued. The *tridactylus* male flew across the stream from the nest, called pik several times, then flew to the southwest, where he continued calling sporadically. A few minutes later the female *arcticus* flew in past the nest, toward the *tridactylus* male. I heard a Scream-Rattle-Snarl, and the Rattle of *tridactylus* and saw the female *arcticus* apparently chasing the male *tridactylus*. All was calm for 10 minutes, and then presumable the same *tridactylus* male again perched near the *arcticus* nest, called pik several times then left, flying toward a distant drumming (of *Picoides*, species uncertain). Later that morning I heard sounds of conflict between the two species in dense spruces south of the *arcticus* nest site, but on my arrival I found the birds, a pair of *tridactylus* and a female *arcticus*, feeding apart. They called sporadically, *arcticus* giving Scream-Rattles and Scream-Rattle-Snarls with partial hunching and half-raising of the wings, and *tridactylus* uttering a Rattle Call. Gradually they foraged farther apart.

In 16 well-observed attack or pursuit situa-

tions, the attacker or pursuer was an *arcticus* male in five cases, an *arcticus* female eight times, a *tridactylus* male once, and a *tridactylus* female twice attacked. On no occasion was an *arcticus* male subjected to an attack, but an *arcticus* female was attacked twice by a *tridactylus* female and once by a *tridactylus* male. Attacks of an *arcticus* male were directed twice at a male, and twice at a female *tridactylus* (in the fifth case I did not determine the sex of the bird attacked). The eight attacks of an *arcticus* female were directed three times at a male, and five times at a female of *tridactylus*. As noted, all three attacks by *tridactylus* were made on a female *arcticus*.

The general dominance of *arcticus*, especially the male, reflects the greater size of *arcticus*, perhaps its greater pugnacity, and probably the fact that most encounters occurred on the territory of a pair of *arcticus*. Two of the three attacks on an *arcticus* female occurred when that female was engaged with a pair of *tridactylus*, and the third attack, an aerial supplanting attack by a female *tridactylus*, resulted in a chase of that female by the supplanted female *arcticus*. Most of the encounters involved the nesting pair of *arcticus*. The rather frequent encounters over this short period of time, the persistence of *tridactylus* even to the point of repeatedly visiting the presumably optimum nesting site chosen by the *arcticus* pair, and the subsequent disappearance of *tridactylus* from the general vicinity, all suggest that the *tridactylus* pair attempted to encroach upon at least part of the territory of the *arcticus* pair, but were unsuccessful, and moved elsewhere to nest.

Reactions of *arcticus* to intruding *tridactylus* (and to other species, of course) was far greater in the vicinity of the nest site than elsewhere in the presumed territory of the *arcticus* pair studied intently. Away from the site, interactions, although sometimes briefly intense, tapered off to a sporadic vocal interaction (permitting both species to feed), or terminated abruptly. It is likely that such feeding specialists as these three-toed woodpeckers may have an easy time securing food in optimum habitats during the breeding season. Nesting sites may be at a premium, however, so that "territorial" defense largely is confined to the vicinity of the nest. This would permit concentrations of these wood-

peckers in loose "colonies," as has been reported (Bent, 1939, pp. 106, 108, 117).

Other Interspecific Encounters of Black-backs

Conflicts occurred between the Black-backed Three-toed Woodpecker and other hole-nesting species, especially the Tree Swallow (*Iridoprocne bicolor*), the congeneric Hairy Woodpecker, and the Common Flicker (*Colaptes auratus*). I noticed two slight interactions between *P. arcticus* and Yellow-bellied Sapsuckers (*Sphyrapicus varius*), one involving a swerving turn in the flight of a nest-bound male *arcticus*, toward a perched sapsucker, which flew off before the *arcticus* drew near, and the other a flight by a sapsucker stimulated by a drumming male *arcticus*. Gibbon (1966, p. 226) noted a "combat" between a female of *P. tridactylus* and a female Yellow-bellied Sapsucker.

Tree Swallows actively investigated holes in trees in the open, and thus were attracted to the nest of the *arcticus* pair. Furthermore the surrounding dead trees invited perching by the swallows, which then could note the woodpeckers' activities and nest. Proximity of the nest to a stream, an open foraging lane for the swallows, also meant frequent passing of this species near the nest. Occasionally a swallow buzzed the nest when the woodpeckers were away. When the woodpeckers were at the nest, however, swallows usually avoided flying too close to it, but there were exceptions.

On May 1, one of three Tree Swallows approached the male *arcticus* as he excavated at the nest, which at this time barely had an entry tunnel, hence was not suitable for nesting by swallows. The swallow darted about, hitting the woodpecker's back with its wings, and causing the *arcticus* to drop down the stub from the nesting cavity. The woodpecker did not display but cautiously moved back to the nest, hanging so that it faced the swallow at all times. There was no repeat performance at this time, but on other occasions a Kyik Call was uttered as a swallow flew by. I noticed that the woodpecker looked about more frequently than usual whenever there were swallows nearby. Gibbon (1966, p. 226) noted the interest of Tree Swallows in the recently vacated nest of a *P. tridactylus*.

I watched from a distance on May 2 as a pair of *arcticus* inspected an old woodpecker hole in a stub near the lake in the middle of the bog. The dead trees in that area comprise a major perching area for the Tree Swallows, and most of their nests were nearby. A group of flying swallows descended to the cavity and besieged the two woodpeckers, one swallow after another darting in and hitting the woodpeckers, which were driven in circles around the trunk. After seven or eight attacks, the woodpeckers flew to the edge of the woods, where they were no longer molested. Moments later one woodpecker, I believe the female, returned to the cavity at lakeside (was this cavity her roosting hole, or a potential roosting hole?), and promptly was attacked by two Tree Swallows, compelling her to leave.

Black-backs responded twice to Common Flickers calling or drumming nearby. On May 3 the male Black-back of the nesting pair was excavating inside the nest when a flicker perched 40 meters away in a stub called. The male *arcticus* immediately responded by coming out of the nest, hopping upward on the nest-containing stub, and drumming four times. The flicker did not call again and flew away within a minute, after which the Black-back returned to its work. A more intense reaction on April 26 occurred when a group of three flickers, engaged in a conflict, landed on a stub about 50 meters from the Black-back nest in preparation. As the flickers called (Wicka Calls) and displayed, the male *arcticus* flew from the nest entrance directly at the two flickers uppermost on the stub, and supplanted them, causing both to fly. Then, Bill Directing downward at the remaining (male; the others were females) flicker, the Black-back attacked and supplanted it, too. The flicker flew 25 meters northeastward, directly away from the Black-back nest, and gave a Long Call (Short, 1972). The male Black-back looked in the direction of the flicker, then, apparently "satisfied," returned to its nest.

Such strong reactions to unrelated or distantly related birds doubtless partly reflect competition for nest sites among hole-nesting birds. Coupled with this factor, persistent weak to strong aggressive reactions to me, and the aggressive nature of interactions within pairs of *arcticus* suggest that selection (or experience) has favored heightened

aggressiveness in *arcticus* compared with at least some other picids, probably as a result of its often exposed nesting sites and openness of the habitat, hence the greater conspicuousness of the birds and their nests.

Two interactions occurred between *Picoides arcticus* and *P. villosus*. These are significant not only from the point of view of the rather close relationship between the three-toed woodpeckers and *villosus*, but because they represent the only occasion in which *villosus* was seen actually within the same area where three-toed woodpeckers occurred. Both incidents took place in June, and probably relate to a shift in feeding patterns of *villosus* after the young leave the nest (*villosus* seems to nest slightly earlier than do the three-toed species, in my limited experience). Gibbon (1966, p. 226) mentioned a "combat" between a male *P. tridactylus* and a female *P. villosus*, but *arcticus-villosus* conflicts have not previously been reported.

On the morning of June 11 a male Hairy Woodpecker flying across the bog-creek area dropped down to perch in a stub 15 meters across the stream from the nest of the Black-backs. The *arcticus* female then flew in to feed, detected the presence of the Hairy Woodpecker, and flew on past the nest at the Hairy, supplanting it by dropping down on it. The male Hairy quickly moved to the other side of the stub. At this, the female Black-back flew to the nest, there to feed the young. Meanwhile, the *villosus* male flew to a distant stub. After feeding, the female Black-back flew to a stub near the nest and drummed once; then she flew toward the *villosus*, giving a Scream-Rattle-Snarl Call, and in Flutter Aerial Display, landed nearly atop the Hairy Woodpecker, supplanting him. Backing away only slightly the male Hairy Woodpecker spread its wings, as did the Black-back, and both made contact, clasped feet, hit with the bill, and tumbled downward holding onto one another. The female Black-back then pursued the male Hairy to another tree nearby, where contact was made once again. Suddenly, giving a Rattle Call (Short, 1971), the Hairy Woodpecker flew off to the south.

The other conflict took place on June 12, also in the morning, and it began with involvement of a female *arcticus* and a male *villosus*. I spied a

male *villosus* feeding in dense bushes across the stream from the *arcticus* nest. It had foraged for 10 minutes when the female *arcticus*, arriving to feed its young, saw the *villosus* and immediately flew at it, attacking and chasing it for a short distance. The *arcticus* female then desisted, and appeared to forage briefly in a dead tree. However, she then resumed chasing the male *villosus* about, until the two landed in a distant stub, about 2 meters apart. At this point the male *arcticus* arrived on the scene, and attacked the male *villosus*, as the female *arcticus*, too, descended the stub and attacked the Hairy Woodpecker. However, the female *arcticus* turned aside as she reached the two wing spreading males. Apparently having had enough, the male *villosus* flew off to the south. Then, the female *arcticus* charged back around the stub, attacking her own mate, and both gave full Scream-Rattle-Snarl Calls and Wing Spreading displays at each other. The pair were at such close range that their spread wings appeared to touch. They quickly separated, and appeared to fly off to forage. The heightened aggression of the female seemed to carry over, causing her to attack her mate after the intruding male *villosus* had flown.

Unfortunately I had only an obstructed view of the birds at close range during these *arcticus-villosus* encounters, and I could detect only the most conspicuous displays and loudest vocalizations. Such displays as Tail Spreading and Crest Raising also may have been used by one or the other, or all three birds. The Hairy Woodpecker is smaller than the Black-backed Three-toed Woodpecker, and overlaps with the Northern Three-toed Woodpecker (personal observ.). The smaller size and transgressions of *villosus* near the nest of *arcticus* partly account for the strong dominance of *arcticus* over *villosus*, but possibly resemblance of some calls and color pattern (head markings, wing pattern) may have influenced the strong response of *arcticus*.

DISCUSSION

Aspects of three-toed woodpecker biology that can be discussed on the basis of the data available at the present time include comparison of the two species with other congeneric species and their relationships. Further data are essential

from other areas, particularly for *Picoides tridactylus* both in North America and in Europe.

This preliminary comparison is based on a considerable volume of data for *arcticus*, representing mainly but one area and one season, and sparser data for *tridactylus* from North America and some published data on that species from Europe. Various vocalizations and displays have been treated above, including comparisons between *arcticus* and *tridactylus*—the reader should consult specific sections for details.

The two species are rather similar in morphology, but are not so similar as are *P. nuttallii* and *P. scalaris*, which hybridize (Short, 1971). In bill structure and size the two three-toed woodpeckers are less different than are *villosus* and *pubescens*. In New York State the three-toed woodpeckers seem attracted to the same wet evergreen forests, but *arcticus* favors more open areas bearing dead trees, whereas *tridactylus* more often is found in the dense spruce-larch forest. The Northern flies less directly, and has a more erratic, wavering flight than does *arcticus*. Both forage similarly, with *arcticus* perhaps doing more direct boring, but *arcticus* forages lower in trees, even onto the ground occasionally, and *arcticus* more often feeds in dead trees and shrubs. The ringing of trees and sapsucking is known in *tridactylus*, but as yet is unknown in *arcticus*. The Black-back probably nests more frequently in open stands of dead trees. Some of these ecological differences undoubtedly are local and not general.

Behaviorally, *arcticus* is much more aggressive and conspicuous than *tridactylus*. The drumming of the latter species is slower, the bursts tend to be shorter, and there is more variation than in *arcticus*. Call notes, which are used in a variety of circumstances, are distinctly different in the two species. The Kweek Call is known only in *tridactylus*, and sounds like Kweek Calls of related species of *Picoides*. If present in *arcticus* it is in highly modified form, as part of the Scream-Rattle-Snarl Call. Rattle Calls of *tridactylus* and *arcticus* are distinctive, being fast and mechanical-sounding in *arcticus*, and slower (resembling other species of *Picoides* in structure and tempo of notes) in *tridactylus*. Other calls cannot be compared because of incomplete data for *tridactylus*. Nevertheless, it appears that *arcticus* and

tridactylus vocally differ considerably. It was found (Short, 1971) that closely interrelated *P. scalaris* and *nuttallii* also showed strong vocal differences. In both situations the interspecific vocal differences much exceeded the differences observed in visual displays.

The three-toed woodpeckers closely resemble other species of *Picoides* in their visual displays. This especially is true of Bill Directing, Crest Raising, the Flutter Aerial Display, and Tail Spreading, although there may prove to be some minor differences (accompanying vocal displays of course usually differ considerably). Bill Lowered and Bill Raised postures are similar in *tridactylus* and *arcticus*, and seem more ritualized than in other *Picoides*; in contrast both species seem to lack a distinct Head Turned Posture, and the Head Bobbing Display of certain other species of *Picoides* (Short, 1971). A Hunched Posture is ritualized in *arcticus*, and is poorly expressed in *tridactylus* (and *villosus*). Head Swinging Displays seem more common in *tridactylus* (and other species of *Picoides*) than in *arcticus*. The Wing Spreading Display is common in *Picoides*, including the three-toed woodpeckers, but is emphasized much more in *arcticus* than in *tridactylus*. Indeed, it is combined in a characteristic manner with the Hunched and Bill Lowered postures, and with a complex (scream) vocalization in *arcticus*.

The strong, and lengthy interactions observed between *tridactylus* and *arcticus*, as well as their morphological and ecological similarities, indicate that these closely related woodpeckers are highly competitive. Probably they overlap greatly in their diet and foraging modes, and both prefer similar habitats. Interspecific territoriality seems to occur, thus resembling the situation involving *P. scalaris* and *P. nuttallii* (Short, 1971). In contrast to the latter situation, *tridactylus* and *arcticus* apparently do not hybridize, and they differ somewhat in size. Morphological differences between the interacting species in each case seem comparable, other than size differences, but vocal and visual displays appear to differ more between the three-toed woodpeckers than between *scalaris* and *nuttallii*. Nevertheless, the similarities between the three-toed woodpeckers are great, and probably are reflected in the rarity of their actual sympatry, despite their great range

overlap and the apparent sympatry it implies.

I previously suggested (Short, 1971, pp. 109, 111, 113-114) that the three-toed woodpeckers are congeneric with other pied woodpeckers ("*Dendrocopos*"), and I discussed their evolutionary history. Goodwin (1968, pp. 32-33), although not merging *Dendrocopos* in *Picoides*, recognized the three-toed woodpeckers as close relatives of North American species of *Dendrocopos*. Results of the present study strongly corroborate my earlier conclusion that the three-toed woodpeckers indeed are closely related to, and congeneric with, the pied woodpeckers. They further extend that conclusion, indicating that *arcticus* has diverged more than has *tridactylus* from the common ancestor of the three-toed woodpeckers.

The morphology, general behavior, and aspects of displays clearly indicate a close similarity with other pied woodpeckers. The habits (and morphology, e.g., loss of a toe) of the three-toed woodpeckers doubtless have been modified as a result of adaptation to existence in northern, coniferous forests only marginally occupied by their New World relatives. Despite their divergence in some respects, the entire array of their displays is akin to that of other congeneric species. The drumming, call notes, presence of a Kweek Call (in at least *tridactylus*), details of the Rattle Call (that of *tridactylus* virtually identical to that of *P. canicapillus*), and even the begging calls of young *arcticus*, all match or are comparable with those of *Picoides villosus* and its relatives. In cases involving differences in vocalizations, the three-toed woodpecker vocalizations are derivable from and show similarities to known vocalizations of *villosus* and other allied species.

The displays of *tridactylus* and *arcticus* include most of the array found in other congeneric species, and the displays are used in roughly comparable situations in the various species. The Bill Directing and Bill Raised postures, the extended Hunched Posture, the Crest Raising Display, the Head Swinging Display, the Tail Spreading Display, and the Wing Spreading Display all show similarity in their details among the species of *Picoides*. None of these is restricted to *Picoides*, but the particular visual display repertoire in which they occur is unique to this genus

(and perhaps closely allied African *Dendropicos*). The Flutter Aerial Display is characteristic of *Picoides*, and its occurrence in the three-toed woodpeckers, as well as its exact resemblance in form to that of *P. villosus*, *pubescens*, and allied species are evidence of relationship with those species. Certainly the behavior of the three-toed woodpeckers bears no close resemblance generally or in details to any other group of woodpeckers.

When taken in the context of morphological and behavioral diversity among the pied woodpeckers (e.g., consider the *P. major* group, *P. hyperythrus*, the *P. maculatus-temminckii* group, *P. doriae*, and others), the loss of a toe and yellow replacement of red in the crown of males hardly seem reasons to separate the three-toed woodpeckers generically from other pied woodpeckers. I call attention again (see Short, 1971, p. 107) to the picid genus *Dinopium*, which contains three-toed and four-toed species, and even one species (*D. shorii*) having either three or four toes. Also, some species of *Picoides* (e.g., *mahrattensis*, *darjellensis*) have pronounced yellow and red about the head, and the allied *Dendropicos* contains species with red on the crown of males, but *D. xantholophus* is yellow-crowned (its allospecies, *pyrrhogaster*, is red-crowned, Short, MS). Given such variation in other picid genera, the three-toed woodpeckers seem to be no more well-marked than are some other species and species-groups (mentioned above) of "*Dendrocopos*." Their recognition as a genus apart from *Dendrocopos* could be defended only if one were to split further that genus into five or six genera. If we recognize this assemblage as monophyletic, it seems best to treat the species as congeneric, stressing their interrelationship and their overall similarities.

When one looks at the three-toed woodpeckers as derivatives of an ancestral species of *Picoides*, it is apparent that in several features *tridactylus* has diverged less than has *arcticus*. One finds as specializations of *arcticus*: the shortened, metallic call note; the fast, short-noted Rattle Call; incorporation of several rattle variations, and perhaps a modified Kweek Call into a complex Scream-Rattle-Snarl Call; a more ritualized Hunched Posture; greater emphasis on Wing Spreading Displays; and evolution of a

complex Wing Spreading-Hunched-Bill Lowered-scream, composite display. Further, there is a definite progression from the condition of, say *Picoides villosus*, through *tridactylus* to *arcticus* in: the reduction of (and possibly modification of) the Kweek Call, which is lacking in *arcticus*; the ritualization of the Hunched Posture; and the reduction of the Head Swinging Display.¹ Goodwin (1968, p. 33) noted that *tridactylus*, particularly its Eurasian forms, is morphologically more like other North American species of *Picoides* than is *arcticus*.

The more specialized behavior of *arcticus* makes sense when one considers the probable history of the three-toed woodpeckers (see Short, 1971, pp. 113-114). The ancestral three-toed woodpecker evolved in northern North America from an ancestor in common with that of the *villosus* group. Sometime, perhaps shortly after it evolved, a population was able to cross Beringia and colonize Eurasia, where it became isolated from its North American populations. The Eurasian form, ancestral *tridactylus*, encountered rather distantly related species of *Picoides* (e.g., species of the *P. major* group), and was able to spread widely in Eurasian coniferous forests. Subsequently, partial or complete isolation led to the evolution of several rather distinct populations (eight Eurasian subspecies are known, Vaurie, 1965). Despite differentiation, there was no strong selective force due to competitive interactions, or the need for enhancement of reproductive isolation, and hence behavioral divergence from the ancestral form probably was minimal.

The North American populations, in contrast, were in direct and lengthy contact with such relatives as ancestral *P. villosus* (and later with *pubescens* and *albolarvatus*). Selection doubtless favored greater behavioral divergence (and probably increased size, including bill size) of ancestral *arcticus* under these circumstances, reducing interactions and leading to the specializations evi-

dent in modern *arcticus*. More recently, *tridactylus* was able to reinvade its ancestral North American home via Beringia. It apparently was reproductively isolated from *arcticus*, but strong competitive interactions and perhaps some reinforcement of reproductive isolating mechanisms probably occurred. As *tridactylus* successfully extended its range across the taiga, it contacted other, related species of *Picoides*. Factors enabling *tridactylus* to compete successfully and occasionally to coexist with *arcticus* perhaps placed a burden upon it in contact with these other species, for divergence in the direction of *arcticus* clearly was impossible. Thus, it is no accident that *tridactylus*, having entered North America, but showing less divergence than *arcticus* from related Nearctic species, occupies a more northern range, and thus is in more limited contact with congeneric species than is *arcticus*.

Probably *arcticus* suffered a reduced range and diminished numbers as a consequence of the invasion of North America by *tridactylus*. The two species, whatever their ecological differences (detailed foraging observations are needed to demonstrate these differences), prefer similar habitats. Hence it is not surprising that they rarely are found together, but rather, one is relatively common in a given region and the other is uncommon, rare, or absent. The behavioral dominance of *arcticus* indicates that it tends to displace *tridactylus*, assuming its preferred habitat and relegating *tridactylus* to secondary habitats wherever the two occur together. The competitive success of *tridactylus* in certain regions probably relates to its foraging efficiency (perhaps in winter, giving it an advantage in colder weather) and perhaps its ability to utilize more diverse habitats.

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¹It is inconceivable that these trends have gone in the other direction, that is, that the three-toed woodpeckers gave rise to other species of *Picoides* (the three-toed condition has evolved independently in four small, distinct groups of woodpeckers, and it clearly is the derived condition in *P. arcticus* and *P. tridactylus*).

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